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A Phylogenetic Study of Living and Fossil Platyrrhines

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ABSTRACT

A phylogenetic analysis of the 16 genera of living platyrrhines (New World monkeys) and 20 fossil taxa of the same group was undertaken. Analyses were conducted on two data sets: one was restricted to morphological characters and the other was a combination of those morphological characters and DNA sequence characters belonging to the 16S and 12S mitochondrial genes and the ε-globin and IRBP nuclear genes. In neither case could all taxa be included without large loss in resolution when the strict consensus trees were computed: the maximum number of fossil taxa that could be included was 11 with the first data set, and 18 with the second; relationships differed between the two. In the simultaneous analysis of morphological and molecular data, relationships among Recent taxa remained invariant regardless of what fossil taxa were included. This allowed a comparison of character changes along branches between a tree including Recent taxa only and a tree including the fossil species and to evaluate the influence that the addition of fossils has on our understanding of character evolution. When fossils were added, branch support values decreased substantially (i.e., for callitrichines and pitheciins) with the following contributing factors: (1) characters were not as clustered in some nodes as in the phylogeny of Recent taxa only but scattered among a larger number of nodes; (2) high numbers of fossils had missing entries, which contributed to their being ubiquitous and accommodating in many topologies; and (3) adding taxa increased the degree of homoplasy and in some cases caused a higher instability for some clades. It is apparent that a high Bremer value may be the result of extinctions and taxonomic incompleteness, rather than correspondence to reality.

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INTRODUCTION

Fossil platyrrhines are known from only a few, widely separated regions of South America and the Greater Antilles. There is almost no overlap between the distribution of extant platyrrhines and the sites that have yielded fossil monkeys. Only the middle Miocene Honda Group in Colombia and a few sites of various ages in Brazil are near areas where monkeys currently live.

The rocks yielding fossil platyrrhines can be divided into five groups based on geographical and temporal grounds (Fleagle et al., 1997). They are, from oldest to youngest: (1) late Oligocene–middle Miocene Salla beds in Bolivia; (2) early to middle Miocene rocks in southern Argentina and Chile; (3) middle Miocene Honda Group rocks in Colombia; (4) late Miocene rocks from Río Acre, Brazil; and (5) Pleistocene–Recent cave deposits in Brazil and the Caribbean. There is one addition to this list: a single remain of early Miocene age from Cuba (MacPhee and Iturralde-Vinent, 1995). The earliest record of fossil primates in South America comes from a late Oligocene level of the Salla beds, Bolivia, dated at 25.82 to 27.02 Ma (Kay et al., 1998).

The Importance of Fossils in Phylogenetic Analysis

Whether fossils can make any contribution to our understanding of the relationships among Recent taxa is a hotly debated issue in systematics. Some investigators believe that fossils play a secondary role in phylogenetic reconstruction (Hennig, 1966; Patterson, 1981; Goodman, 1989), but their importance has been demonstrated in the cases described below.

The most striking influence of fossils is probably exemplified by the phylogenetic relationships of birds and mammals. When no fossils are included in an amniote phylogeny, mammals and birds appear as sister taxa (Gardiner, 1982; Gauthier et al., 1988). With the inclusion of fossils, birds appear closer to crocodiles than to mammals among Recent taxa (Gauthier et al., 1988; but see Gardiner, 1993). To explore the reasons for the change in relationships, Gauthier et al. (1988) designed a series of computer experiments that deleted groups of fossils from the analysis. They concluded that fossil outgroups alone (in other words, deleting all the fossil ingroups) were not sufficient to cause the change in position of the mammals seen in the complete analysis. Among the fossil ingroups, only the inclusion of synapsid fossils was responsible for the change in position of the mammals. Among these, addition of the earliest or latest synapsid groups did not alter the Recent tree; only addition of intermediate taxa (even a single addition) was sufficient to recover the topology for extant groups implied by the complete analysis. Their explanation for this emerged from an analysis of the distribution of characters on the complete tree. Living mammals and archosaurs acquired many postcranial characters independently, including modifications in the girdles, limbs, and vertebral column that presumably enabled them to acquire an erect posture and a narrow-tracked gait, which in turn facilitated breathing while running. In this case some synapsid fossils provided intermediate character states and new combinations of characters that resulted in altered topologies from those based on Recent taxa only.

Novacek (1992) observed a similar situation in his analysis of higher mammal relationships, particularly among perissodactyls, hyracoids, and tethytheres. In an analysis of Recent taxa only, hyracoids grouped with perissodactyls, whereas when fossil ingroups were added, hyracoids shifted to a closer relationship with Tethytheria (proboscideans and sirenians). Inclusion of early perissodactyls such as *Hyracotherium* was crucial for this change in topology. Although fossil horses share autapomorphies with extant perissodactyls, the former were more primitive for other characters shared by hyracoids and living perissodactyls. In the more complete analysis, the close link between *Hyracotherium* and living perissodactyls was stronger than the similarity shared by hyracoids and living perissodactyls, which become homoplasious. In addition, the evidence supporting a sister-group relationship between hyracoids and tethytheres was such that addition of a primitive perissodactyl was enough to overturn the topology of the tree. As in the case of amniotes, fossils provided combinations

of characters that were not found in any Recent taxa and were crucial in the resolution of certain relationships.

In the case of the phylogeny of seed plants, inclusion of fossils in the analysis also has an effect on the relationships among Recent taxa (Doyle and Donoghue, 1986, 1987, 1992; Loconte and Stevenson, 1990; Nixon et al., 1994). Nixon et al. (1994) found that living *Gingko* is the sister group of a clade formed by conifers, gnetopsids (which turns out to be a paraphyletic group), and angiosperms. Inclusion of fossils yielded additional most parsimonious results, where *Gingko* was outside the conifer clade + anthophytes (gnetopsids and angiosperms) in some trees, whereas in others it was a member of a broader "conifer" clade.

On the other hand, fossils may have an undesirable effect by considerably decreasing resolution when consensus trees of all most parsimonious trees are computed (Rowe, 1988; Greenwald, 1989; Novacek, 1992). This is a consequence of the proliferation of question marks for many character states that are impossible to determine in fossil taxa, or are unknown because some parts are not preserved. Taxa that can be placed in any one of several equally parsimonious positions on cladograms will cause nodes located between the possible positions to collapse when phylogenetic trees are combined in consensus trees. This was the case with the relationships among the orders of mammals (Novacek, 1992, 1994). When the number of fossils are gradually increased in a data set formed mostly by Recent taxa, the increase in the number of trees follows approximately an exponential function (Novacek, 1994; Forey, personal commun.).

Whatever the source or amount of missing information, Donoghue et al. (1989) pointed out that completeness and informativeness are not strictly coupled. Taxa that can be scored for every character are not necessarily especially relevant in answering specific phylogenetic questions, whereas taxa that are rather poorly known may nevertheless reveal combinations of characters that are critical in establishing relationships. Therefore, it is not possible to predict the effect of adding a fossil (or fossils) to a phylogeny.

The effects of the inclusion of the New World monkey fossil taxa in the complete Recent generic data set have now been studied. Previous studies addressed the phylogenetic relationships of isolated fossil taxa but they did not include them simultaneously in a phylogenetic analysis. There are at least 23 species of fossil New World monkeys known from dental remains, with some from other parts of the skeleton. I review here the fossil platyrrhine species and I present a phylogenetic analysis including them and all Recent genera.

Abbreviations

Institutional

AMNHM	American Museum of Natural History, Department of Mammalogy
CENDIA	Centro Dominicano de Investigaciones Antropológicas
DU	Duke University
FML	Museo de la Fundación Miguel Lillo, Tucumán, Argentina
IGM	Museo Geológico del Instituto Nacional de Investigaciones Geológico-Mineras, Bogotá
KU	Kyoto University
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MACN-CH	——, Chubut collection
MACN-SC	——, Santa Cruz collection
MLP	Museo de La Plata, Argentina
MNHNH	Museo Nacional de Historia Natural, La Habana, Cuba
MNHN-Bol	Museo Nacional de Historia Natural de Bolivia, La Paz
UCMP	University of California Museum of Paleontology, Berkeley, California
UF	University of Florida
USNM	United States National Museum of Natural History

Other

C	Canine
ch.	character
CI	Consistency index
I	Incisor
M	Molar
P	Premolar
RI	Retention index

MATERIALS AND METHODS

All genera of Recent and most fossil species of New World monkeys plus several out-

groups were included in this analysis, as shown in table 1. *Neosaimiri fieldsi* and *Laventiana annectens* were pooled in a single terminal taxon. Based on similarities between the two (Takai, 1994; Kay and Meldrum, 1997), they are considered here to be sister taxa; the type specimens include only lower dentition; upper teeth were recovered in subsequent years, and it is not possible to tell which of the two species they belong to (Takai, 1994). This is the reason why they are treated here as a single terminal taxon. *Branisella boliviana* and *Szalatavus attricuspis* were also pooled because *Szalatavus* is represented by few remains with many missing character entries. While some authors consider the two species to be synonymous (Takai and Anaya, 1996), the authors of *Szalatavus* consider it to be the sister group of *Branisella* (Rosenberger et al., 1991b). For present purposes, both are reasons enough to pool them in a single terminal taxon.

Micodon kiotensis (Setoguchi and Rosenberger, 1985) was excluded because of the scarcity of remains; the type is a single isolated upper molar, with an upper incisor and a lower premolar tentatively referred to it. Species such as *Chilecebus carrascoensis* (Flynn et al., 1995), *Protopithecus brasiliensis* (Lund, 1838; Hartwig, 1995a, 1995b), and *Caipora bambuiorum* (Cartelle and Hartwig, 1996) were omitted because they are not yet completely described and are still under study by their authors.

Two separate sets of analyses were conducted: the first included morphological characters only, and the second was based on a combined data set that included the morphological characters and molecular DNA sequence data of nuclear and mitochondrial origin. The morphological data set included 86 characters, mostly skeletal. These are listed in appendix 1 (see also Horovitz and MacPhee, 1999) and the corresponding data matrix is shown in appendix 2. Characters with multiple entries for a taxon were considered polymorphic in the phylogenetic analyses.

All DNA sequences have been previously published. The nuclear DNA sequences belong to two different sets of genes: ε-globin genes (261 informative sites; see Schneider et al., 1993) and the interstitial retinoid-binding protein gene (IRBP) intron 1 orthologues (332 informative characters; see Harada et al., 1995, and Schneider et al., 1996). Mitochondrial sequences included a fragment of the mitochondria-encoded 16S ribosomal gene (142 informative characters; see Horovitz and Meyer, 1995) and the entire 12S ribosomal gene (324 informative characters; see Horovitz et al., 1998). All molecular plus

TABLE 1
Ingroup and Outgroup Taxa Included in Phylogenetic Analyses

Ingroups
16 LIVING GENERA
BOLIVIAN LATE OLIGOCENE—EARLY MIOCENE FOSSILS
Branisella boliviana
Szalatavus attricuspis
ARGENTINE PATAGONIAN EARLY—MIDDLE MIOCENE FOSSILS
Carlocebus carmenensis
Carlocebus intermedius
Dolichocebus sarmientoi
Homunculus patagonicus
Soriacebus adrianae
Soriacebus ameghinorum
Tremacebus harringtoni
COLOMBIAN MIDDLE MIOCENE FOSSILS
Aotus dindensis
Cebupithecia sarmientoi
Lagonimico conclucatus
Laventiana annectens
Mohanamico hershkovitzi
Neosaimiri fieldsi
Nuciruptor rubricae
Patasola magdalenae
Stirtonia tatacoensis
Stirtonia victoriae
CARIBBEAN QUATERNARY FOSSILS
Antillothrix bernensis
Paralouatta varonai
Xenothrix mcgregori
Outgroups
LIVING TAXA
Tarsius syrichta (root)
Hylobates lar
Homo sapiens
Cercopithecoids
EGYPTIAN OLIGOCENE FOSSIL
Aegyptopithecus zeuxis

most morphological data for Recent genera have been analyzed previously (Horovitz et al., 1998).

DNA sequences were aligned with Malign 1.89 (Wheeler and Gladstein, 1993) and gaps were treated as described elsewhere (Horovitz and Meyer, 1997; Horovitz et al., 1998). Aligned molecular sequences and morphological characters were analyzed with PAUP 3.1.1 (Swofford, 1993), applying heuristic searches, using initial trees obtained with random stepwise addition of taxa; the minimal trees were submitted to tree bisection and reconnection (TBR); the process was repeated 100 times. Searches including the largest number of taxa (38 to 41 taxa) were double checked using the parsimony ratchet (Nixon, presentation at the "One Day Symposium on Numerical Cladistics," New York, 1998), as implemented in NONA 1.9 (Goloboff, 1998). This procedure is very effective at finding multiple islands of trees and potentially the global optimum. The command used in NONA was nixwts*10 100; this command performs 10 iterations of the ratchet and every time an iteration is completed, it creates 100 random addition sequence Wagner trees and uses the shortest one(s) for the next iteration. The results were consistent with those obtained with PAUP. Bremer supports (Bremer, 1988; Källersjö et al., 1992) were calculated inspecting the strict consensus of trees up to 22 steps longer than most parsimonious ones including Recent platyrrhines only and 5 steps longer than the tree including fossils.

Several named higher taxa are discussed here and they are defined as follows: Ateloidea includes pitheciids and atelids; Atelidae includes *Ateles*, *Brachyteles*, *Lagothrix*, and *Alouatta* and related fossil species; Pitheciidae includes *Callicebus*, related fossil species, and pitheciines; Pitheciinae includes *Nuciruptor*, *Cebupithecia*, *Pithecia*, *Cacajao*, and *Chiropotes*; Pitheciini includes *Pithecia*, *Cacajao*, and *Chiropotes*; Ceboidea includes *Cebus*, *Saimiri*, *Aotus*, callitrichines, and all fossil species descended from internal nodes of this clade; Callitrichinae includes *Callimico*, *Saguinus*, *Leontopithecus*, *Callithrix*, *Cebuella*, and all fossil descended from internal nodes of this clade; and Callitrichini includes *Callithrix*, *Cebuella*, *Leontopithecus*, and *Saguinus* (group valid in morphological analyses only).

REVIEW OF CRANIODENTAL REMAINS OF FOSSIL TAXA AND PREVIOUSLY PROPOSED RELATIONSHIPS

Bolivian Late Oligocene–Early Miocene

Branisella boliviana Hoffstetter, 1969

Provenance: Type specimen from Salla beds of late Oligocene–early Miocene age of Bolivia, locality unknown; referred specimens come from a late Oligocene level, Salla beds (Kay et al., 1998).

Specimens: Type specimen: left maxilla with P^4-M^2 and roots for P^{2-3}. Referred specimens: P^3 or P^2 and fragmentary maxillae with M^{1-2} and root for M^3 (MNHN-Bol-V 3460, 3466-7); various mandibles with M_1, M_2, $M_{1,2}$, and roots and/or alveoli for P_{2-4}, M_1, and M_3 (MNHN-Bol-V 3463-5, 3468-9, 3471, PU 21861).

Affinities: Two major hypotheses have been proposed: one is that *Branisella* is close to the ancestral platyrrhine (Orlosky, 1973; Rosenberger, 1979b; Conroy, 1990) and the other that it is related to callitrichines (Takai and Anaya, 1996). Another species, *Szalatavus attricuspis*, has been described from the same locality where *Branisella* was found (Rosenberger et al., 1991b) but some authors consider this species a junior synonym of *Branisella* (Takai and Anaya, 1996). Given that *Szalatavus* is represented by few remains with many missing character entries and is considered by its authors to be the sister group of *Branisella*, both species are here pooled into a single terminal taxon.

Szalatavus attricuspis Rosenberger et al., 1991b

Provenance: Late Oligocene level, Salla beds, Bolivia.

Specimens: Type specimen: maxilla fragment with M^{1-3} (UF 27887) and mandible with M_2 (UF 27888). Referred specimen: mandible fragment with M_{2-3}(UF 91399).

Affinities: See *Branisella boliviana*.

ARGENTINE PATAGONIAN EARLY–MIDDLE MIOCENE

Carlocebus carmenensis Fleagle, 1990

PROVENANCE: Early Miocene, Pinturas Fm., Santa Cruz Province, Argentina.

SPECIMENS: Type specimen: mandible fragment with P_4-M_2 and alveoli for $P_{2,4}$ and M_3 (MACN-SC 266). Referred specimens: fragments of maxillae and mandibles with I_2-M_3 and P_3-M_3; isolated I^2-M^3, dP^4, and C_1-M_3 (MACN-SC 1, 11, 43, 44, 63, 90, 98, 99, 100, 103, 104, 105, 230, 236, 248, 250, 252–4, 264–6, 270, 283, 284, 286, 305, 306, 309, 314, 317, 325–7, 370, 378, 382, 383, 400; unpubl.: 10, 22, 23, 26, 27, 41, 45, 46, 48, 52, 54, 60, 66, 76, 80, 92, 109, 112, 115, 232, 243, 257, 292, 296, 318, 321, 328, 354, 370, 375)

AFFINITIES: Fleagle (1990) found that *Carlocebus* shows the greatest similarities with *Callicebus* in both the upper and lower molars and in the presence of hypocones on P^{3-4} but it differs from it in the relatively smaller incisors and in having more prominent cingula in upper premolars and molars. Likewise, *Homunculus* seemed to be closely related to *Carlocebus*.

Carlocebus intermedius Fleagle, 1990

PROVENANCE: Early Miocene, Pinturas Fm., Santa Cruz Province, Argentina.

SPECIMENS: Type specimen: mandibular fragment with C_1-M_2 (MACN-SC 3). Referred specimens: mandibular fragment with P_{2-4}, isolated C_1, P_3 (MACN-SC 3, 280; unpubl.: 81, 259, 289).

AFFINITIES: Sister group of *C. carmenensis* (Fleagle, 1990).

Dolichocebus gaimanensis Bordas, 1942; Kraglievich, 1951

PROVENANCE: Early Miocene, Gaiman, Chubut Province, Argentina.

SPECIMENS: Type specimen: distorted and edentulous skull (MACN 14128). Referred specimens: I^2, C, P^3, $M^{1,3}$, C_1, P_2 (MACN-CH 356, 357, 359, 361; unpub. 256, 358, 871, 877, 878, 898, 899, 1011, 1012, P^4 Duke specimen).

AFFINITIES: Rosenberger (1979a, 1982) argued that the interobital foramen in *Dolichocebus* is a clear indication of its affinity with *Saimiri*; however Hershkovitz (1970, 1982) pointed out that this apparent interobital septum foramen may not be such, but the result of breakage. The specimen is very badly damaged in this area and it was not possible to determine in the present study if the foramen is natural or an artifact.

Based on the dentition, Fleagle and Bown (1983) found many characters in *Dolichocebus* to be very primitive, more than in any other platyrrhine, living or fossil. These include upper dentition hypocone, cingulum, stylar region, and paraconules. They found the most resemblance with an Oligocene anthropoid from Fayum, Egypt, *Aegyptopithecus*.

Homunculus patagonicus Ameghino, 1891

PROVENANCE: Early–middle Miocene, Santa Cruz Fm., Santa Cruz Province, Argentina.

SPECIMENS: Type specimen: mandible with I_2-M_2 (MACN 634). The systematics of this genus and other monkey remains recovered by Carlos Ameghino from the same geographical area await revision. As a preliminary approach, all remains are here pooled in a single terminal taxon. Referred specimens: facial portion with orbit and worn out toothrow; cranial portion with part of the face and cranial cavity; mandibular fragments with M_{1-2}; isolated C_1 and dP_4, P^3, $M^{1,2}$ (MACN 5757, 5986, 5966, 635, 3026, 3099, 2918, 5969, 10403, 8648 [=*Stilotherium*], MACN SC-336, 338, 339; MLP-11-121, MLP-55-XII-13-151, CORD-PZ 1130; unpubl. MACN SC-334, 337, 342, 402, 3112).

AFFINITIES: Many possible affinities have been suggested for *Homunculus*: with *Callicebus* (Rosenberger et al., 1990), *Alouatta* (Hershkovitz, 1970, 1981, 1984), pitheciins (Tauber, 1991), or *Carlocebus* (Fleagle, 1990).

Soriacebus adrianae Fleagle, 1990

PROVENANCE: Early Miocene, Pinturas Fm., Santa Cruz Province, Argentina.

SPECIMENS: Type specimen: partial mandible with $P_{3,4}$, roots of C_1 and P_2, and alveoli for incisors (MACN-SC 59). Referred specimens: maxilla with $P^{2,3}$; mandible fragment with P_4-M_1; isolated I-M_2, P^2 and M^2

(MACN-SC 59, 94, 106, 249, 251, 258, 260, 263, 269, 344, 371, 389, 1154; unpubl.: 24, 30, 47, 118, 242, 268, 299, 300, 330, 351, 393).

AFFINITIES: Sister group of *S. ameghinorum*.

Soriacebus ameghinorum Fleagle et al., 1987

PROVENANCE: Early Miocene, Pinturas Fm., Santa Cruz Province, Argentina.

SPECIMENS: Type specimen: right mandibular ramus with P_2-M_3 and roots for left and right I_1-C_1. Referred specimens: maxilla with C^1-M^2, mandibular fragments, and isolated C_1-M_3, isolated C^1-M^2 (MACN SC-2, 4, 33, 37, 61, 67, 82, 285, 379, *Soriacebus* cf. *ameghinorum* MLP 69-III-12-1; unpubl.: MACN SC-5, 8, 18, 25, 35, 36, 39, 42, 62, 68, 78, 116, 237, 238, 241, 265, 373, etc.).

AFFINITIES: According to several authors, *Soriacebus* shares several features with phyletically unrelated platyrrhines (Fleagle et al., 1987; Rosenberger, 1988; Fleagle, 1990; Kay, 1990; Rosenberger et al., 1990): it shares features of the anterior mandibular dentition with pitheciins, such as large canines, mesiodistally short incisors, and tall P_2; it shares the presence of tall lower incisors and hypocones in premolars with *Callicebus*; and the morphology of the mandibular premolars and long molar trigonids with callitrichines. Rosenberger et al. (1990) were inclined toward placing it within Pitheciini. Kay (1990) and Kay and Meldrum (1997) considered it an early offshoot of platyrrhines.

Tremacebus harringtoni Hershkovitz, 1974 (previously *Homunculus harringtoni* Rusconi, 1933)

PROVENANCE: Early Miocene (Colhuehuapian), Sacanana, Chubut Province, Argentina.

SPECIMENS: Type specimen: complete but broken skull, with two shattered molars (FML 619). Referred specimens: mandibular fragment with part of P_4 and M_1, and alveoli for C_1-P_3 and M_2 (MACN-CH 354) (Fleagle and Bown, 1983), though Fleagle (1990) has reassigned this specimen to *Soriacebus* sp. This mandible displays one difference from *Soriacebus*: its M_1 oblique cristid intersects the protolophid in a position lingual to the protoconid, whereas in *Soriacebus* it is directly distal to the protoconid (see ch. 52, appendix 1). Therefore, following Fleagle and Bown (1983; contra Fleagle, 1990), it is referred to *Tremacebus*.

AFFINITIES: In spite of being broken, *Tremacebus* seems to have large orbits. Based on this character, Szalay and Delson (1979) suggested that it could be related to *Aotus*. Hershkovitz (1974) considered it a very primitive platyrrhine.

COLOMBIAN MIDDLE MIOCENE

Aotus dindensis Setoguchi and Rosenberger, 1987

PROVENANCE: Middle Miocene, Honda Group, La Venta, Colombia.

SPECIMENS: Type specimen: mandible with I_1-M_3 (IGM-KU 8601).

AFFINITIES: This species was considered by its discoverers to be a close relative of the living owl monkey of the same genus. Kay (1990), however, suggested that *Mohanamico hershkovitzi* and *Aotus dindensis* were synonymous and that they were most likely close relatives of pitheciins, less likely of *Callimico*, and least compellingly of *Aotus* (but see Fleagle et al., 1997). In a more recent paper Meldrum and Kay (1997) considered that an affinity with pitheciins is less likely, and suggested that an allocation of *Mohanamico* to Callitrichinae is an alternative worth exploring.

Cebupithecia sarmientoi Stirton and Savage, 1951

PROVENANCE: Middle Miocene, Villavieja Fm., La Venta area, Colombia.

SPECIMENS: Type specimen: part of right maxilla with C^1 and P^3-M^2; left maxilla and part of premaxilla with P^3-M^2, root of I^1, alveolus of I^2, basal part of C^1, alveoli for P^2 and M^3, most of palatal region and lower edge of orbit; left petrosal with part of zygomatic and glenoid attached; right petrosal with part of condyle attached. Mandible with left C_1, P_3-M_1 and right $P_{3,4}$; alveoli for $I_{1,2}$, P_2, $M_{2\text{-}3}$; several postcranial remains (UCMP 38762). Referred specimens: right maxilla with C^1 and P^2 (IGM-KU 8602).

AFFINITIES: The authors of this species (Stirton and Savage, 1951) and Stirton (1951), as well as Orlosky (1973), Rosenberger (1979b), and Kay (1990) held that it is a pitheciin based on similarities shared with all members of this group. The absence of additional derived characters shared with individual pitheciins suggested that *Cebupithecia* is the sister group of the whole group. Hershkovitz (1970) maintained that the characters cited by Stirton and Savage (1951), such as the procumbency of the maxillary incisors and lateral eversion of the maxillary canines, are the result of postmortem damage. Examination of the specimen, however, does not reveal deformations.

Lagonimico conclucatus Kay, 1994

PROVENANCE: Middle Miocene, La Victoria Fm., La Venta area, Colombia (Kay, 1994).

SPECIMENS: Represented by a single specimen consisting of a crushed skull with left I^2, P^2-M^3, right I^1, C-P^4, and mandible with left I_1-M_3 and right C_1-P_4 and M_{2-3} (IGM 184531).

AFFINITIES: Kay (1994) performed an exhaustive search with PAUP, that included *Callithrix*, *Leontopithecus*, *Saguinus*, *Callimico*, *Aotus*, *Callicebus*, *Pithecia*, and *Lagonimico conclucatus*, and 18 characters, which yielded three most parsimonious trees; in all of them *Lagonimico* is the sister group of (*Callithrix*, *Saguinus*, *Leontopithecus*).

Laventiana annectens Rosenberger et al., 1991c

PROVENANCE: Middle Miocene, Villavieja Fm., La Venta, Colombia.

SPECIMENS: Type specimen: mandible with right and left C_1-M_2 and alveoli for $I_{1,2}$ and M_3 (IGM-KU 8801a) and associated right talus (IGM-KU 8801b).

AFFINITIES: The authors of this species suggested it may be the sister group of the (*Neosaimiri*, *Saimiri*, *Cebus*) clade (Rosenberger et al., 1991c). Other authors, however, considered it to be congeneric with *Neosaimiri* (therefore referred to it as *Neosaimiri annectens*; see Kay and Meldrum, 1997) or synonymous with *Neosaimiri fieldsi* (Takai, 1994).

Mohanamico hershkovitzi Luchterhand et al., 1986

PROVENANCE: Middle Miocene, Fm. Villavieja, La Venta area, Colombia.

SPECIMENS: Mandible with left I_2, C_1, P_3-M_2, right P_2-M_2, and roots of left I_1 and right I_1-C_1 (IGM 181500).

AFFINITIES: Luchterhand et al. (1986) suggested that this species might be related to pitheciins; they noted, however, that it shares some derived traits with *Callimico* and *Saguinus*, a situation that led them to propose that callitrichines and pitheciins might be a monophyletic group. Rosenberger et al. (1990) were in favor of the hypothesis that *Mohanamico* is a primitive callitrichine, while Kay (1990) argued that it is synonymous with *Aotus dindensis* and is most likely a close relative of pitheciins, less likely of *Callimico*, and finally and least compelling, a relative of *Aotus*. Meldrum and Kay (1997) reconsidered this issue in light of new findings and found evidence that *Mohanamico* is probably not a pitheciin.

Neosaimiri fieldsi Stirton, 1951

PROVENANCE: Middle Miocene, Villavieja Fm., La Venta, Colombia.

SPECIMENS: Type specimen: two mandibular fragments with I_2-M_2 and roots for I_1-C_1, alveoli for M_3 (UCMP 39205). Referred specimens (to this species merged with *Laventiana annectens*): I_1-M_1, dC_1-dP_4, I^1-M^3, dC-dP^4, some associated mandibular or maxillary fragments, others isolated (sample: IGM-KU 89142, 89017, 89009, 89013, 89047, 89008, 89011, 89091, 89048, 89128, 89140, etc.; see Takai, 1994).

AFFINITIES: It has been claimed that *Neosaimiri fieldsi* cannot be distinguished from modern populations of *Saimiri* (Rosenberger et al., 1991a); in this study, however, relevant differences between the two were found (see Discussion; see also Takai, 1994, and Kay and Meldrum, 1997, for similar conclusions). *N. fieldsi* and *Laventiana annectens*, on the other hand, are very similar: some claim they are conspecific (Takai, 1994) others that they are congeneric (Kay and Meldrum, 1997). Stirton (1951) named *Neosaimiri* in the belief that it is the closest relative of *Saimiri*; Kay and Meldrum (1997), however, included

Callithrix, *Saguinus*, *Leontopithecus*, *Callimico*, *Saimiri*, *Callicebus*, *Cebus*, *Aotus* and the fossils *N. fieldsi*, *L. annectens*, and *Patasola magdalenae* in a morphological analysis, and obtained two different positions for *Neosaimiri*: either as sister group of (*Saimiri*, callitrichines), or as the sister group of callitrichines.

Nuciruptor rubricae Meldrum and Kay, 1997

PROVENANCE: Middle Miocene, Honda Group, La Venta, Colombia.

SPECIMENS: Type specimen: partial mandible with left I_1, right C_1-M_2, and alveoli for right I_{1-2} (IGM 251074). Referred specimens: possibly IGM-KU 8602, consisting of a partial maxilla with C^1-P^2 (originally referred to *Cebupithecia sarmientoi* [Setoguchi et al., 1987]; the finding of this new species, however, opens the alternative that it could be referred to *Nuciruptor*), isolated left talus (IGM 184074; see Ford et al., 1991), and specimen IGM 184667, consisting of a partial pelvis and pelvic limbs, originally referred to *Cebupithecia*, but could also be referred to *Nuciruptor*.

AFFINITIES: This species was placed as the sister group of the clade consisting of *Cebupithecia* and the pitheciins by its authors.

Patasola magdalenae Kay and Meldrum, 1997

PROVENANCE: Middle Miocene, La Victoria Fm., La Venta area, Colombia.

SPECIMENS: Mandible with dP_{2-4}, M_1, and M_2 (IGM 184332, type specimen), and I^{1-2}, C, P^4, and M^1 or M^2 (IGM 250829, cf. *Patasola*, table 26.1 in Kay and Meldrum, 1997).

AFFINITIES: Kay and Meldrum (1997) conducted a phylogenetic analysis of a selected group of platyrrhines to investigate the phylogenetic relationships of *Patasola magdalenae*. They included the Recent *Callithrix*, *Saguinus*, *Leontopithecus*, *Callimico*, *Saimiri*, *Callicebus*, *Cebus*, *Aotus*, and the fossils *Neosaimiri fieldsi*, *Laventiana annectens*, and *Patasola magdalenae*. They collected 55 morphological characters and employed the heuristic algorithm of PAUP. Trees were rooted with a clade formed by *Aotus*, *Cebus*, and *Callicebus*. They obtained three most parsimonious trees, where *Patasola* is located within Callitrichinae in two different positions: it is the sister group of either (*Callithrix*, *Saguinus*), or of ((*Callithrix*, *Saguinus*) *Leontopithecus*). The teeth of *Patasola* are among the smallest of New World monkeys, smaller than those of *Callimico* or *Saimiri*.

Stirtonia tatacoensis Hershkovitz, 1970 (previously *Homunculus tatacoensis* Stirton, 1951)

PROVENANCE: Middle Miocene, La Dorada Fm., La Venta area, Colombia.

SPECIMENS: Type specimen: part of mandible with C_1, P_3-M_2, and alveoli for I_{1-2} and M_3 (UCMP 38989). Referred specimens: I_2 and M_2 and P^{2-4}, and M^3 (UCMP 39204; IGM-KU-III-I; IGM-KU 8201, 8202).

AFFINITIES: Stirton (1951) originally allocated this species to the fossil genus *Homunculus*. The same author considered *Homunculus* to be closely related to *Alouatta*. *H. tatacoensis* was later removed to a new genus, *Stirtonia* (Hershkovitz, 1970). Rosenberger (1979b), Setoguchi et al. (1981), and Kay et al. (1987, 1989) suggested that *Stirtonia* is closely related to *Alouatta*; Hershkovitz (1984), however, contended that these two lineages are unrelated.

Stirtonia victoriae Kay et al., 1987

PROVENANCE: Middle Miocene, La Dorada Fm., La Venta area, Colombia.

SPECIMENS: Type specimen: right maxilla and premaxilla with dP^2-dP^4, M^{1-2}; C-P^4 unerupted and roots for I^{1-2}, dC; left dC-dP^4 and M^2, and unerupted C-P^4 (DU/IGM 85-400, 86-534). Referred specimen: maxilla with C-M^2 (DU/IGM 86-057).

AFFINITIES: Sister group of *S. tataconesis* (Kay et al., 1987, 1989). Larger than *S. tatacoensis*, roughly the size of *Alouatta*.

CARIBBEAN QUATERNARY

Antillothrix bernensis MacPhee et al., 1995 (previously *Saimiri bernensis* Rímoli, 1977)

PROVENANCE: Holocene, Cueva de Berna and others, Dominican Republic.

SPECIMENS: Type specimen: partial right

maxilla with P^4-M^2 and alveoli for P^2 and P^3 and part of the alveolus for C^1 (CENDIA 1). Referred specimens: partial mandible with M_1 and alveoli for P_2-P_4 (UF 28038) and partial distal tibia (USNM-Mammals 254682; see Miller, 1929, and Ford 1986a).

AFFINITIES: This species was originally named *"Saimiri" bernensis* because, according to its author, it shared certain similarities with the living genus *Saimiri*; the finding of the mandible led to the idea that it might be related to *Cebus* rather than to *Saimiri* (MacPhee and Woods, 1982); recent cladistic analyses yielded a different result: *Antillothrix* and *Paralouatta* (the latter from Cuba) appear as sister taxa, with *Xenothrix* (from Jamaica) as their sister group (MacPhee et al., 1995; Horovitz, 1997; Horovitz and MacPhee, 1999).

Paralouatta varonai Rivero and Arredondo, 1991

PROVENANCE: Quaternary (?), Sierra de Galeras, Pinar del Río, Cuba.

SPECIMENS: Type specimen: skull with right P^3-M^3 and left P^2-M^3 (MNHNH V194). Referred specimens: partial mandible with right I^2 -C^1 and left P_2-M_3, isolated I^1-M^3, I_1-M_3, and dP^4 (sample: V150, V105, V115, V163, V166, V106, V179-181, V191-2, V126, V195, V127, V117, V118, V119, V195, V123, V195, V124; see Horovitz and MacPhee, 1999).

AFFINITIES: Rivero and Arredondo (1991) suggested that this species might be a close relative of the living genus *Alouatta*, based on size and the overall shape of the skull. MacPhee et al. (1995), Horovitz (1997), and Horovitz and MacPhee (1999), however, conducted cladistic analyses with data obtained with the original skull plus the mandible and the isolated dental remains that were recovered years later, and found *Paralouatta* to be the sister group of *Antillothrix bernensis*, and a member of a clade composed of the three Antillean species (whose third member is *Xenothrix mcgregori*).

Xenothrix mcgregori Williams and Koopman, 1952

PROVENANCE: Holocene, Long Mile Cave and others, Jamaica.

SPECIMENS: Type specimen: mandible with left M_1 and M_2 and alveoli for left P_4-I_1 and right P_3-I_1 (AMNHM 148198). Referred specimens: partial skull with maxillae, ethmoid, palatines, vomer, basisphenoid, premaxillae, left and right P^4-M^2, and alveoli for all other teeth (AMNHM 268006); partial maxilla with P^3-M^2 and alveolus for P^2 (AMNHM 268007); two partial left mandibles, one with P_3-M_2 and the other with M_1-M_2 (AMNHM 268004 and 268001 respectively; see Horovitz et al., 1997; Horovitz and MacPhee, in prep., for referred craniomandibular elements); femur (AMNHM 259900), two tibiae (AMNHM 259902 and 259903), and os coxae (AMNHM 259904; see Ford, 1986a, 1990, and MacPhee and Fleagle, 1991, for postcranial elements).

AFFINITIES: *X. mcgregori* was initially classified as a "cebid" (meaning all platyrrhines except callitrichines) incertae sedis (Williams and Koopman, 1952). Later studies indicated that it is possibly a close relative of *Callicebus* and *Pithecia* (Rosenberger, 1977; Rosenberger et. al, 1990). These studies did not include the other two Antillean species; when these were included together in a cladistic analysis, however, *X. mcgregori* appeared as the sister group of (*Paralouatta-Antillothrix*), with *Callicebus* as the mainland sister group of the Antillean clade (Horovitz, 1997; Horovitz et al., 1997; Horovitz and MacPhee, 1999). Ford (1986a, 1986b, 1990) suggested affinities between *Xenothrix* and the callitrichines, inspired mostly by the tibia and the dental formula.

RESULTS

MORPHOLOGICAL ANALYSIS

POSITIONS OF THE FOSSIL TAXA

All taxa were included in tree calculations: in a first run they were included all at once and in subsequent runs fossil taxa were sampled individually and in different combinations. *Tarsius* was designated as the root, and in all trees except when noted, *Aegyptopithecus* branched off next to the root, and living catarrhines formed a monophyletic group, sister to the platyrrhines. Two results were evaluated in each run: the position of fossil

taxa in the trees and their influence in the topology of the relationships among Recent and other fossil taxa.

It is possible to include a maximum of 11 fossil taxa at once in an analysis without substantial loss of resolution. Two combinations of 11 taxa were possible–these two sets differ only by one taxon; in one case (α) *Carlocebus carmenensis* was included, in the other (β) *Branisella boliviana/Szalatavus attricupis*. The taxa common to both data sets are, in alphabetical order: *Antillothrix bernensis*, *Cebupithecia sarmientoi*, *Lagonimico conclucatus*, *Mohanamico hershkovitzi*, *Nuciruptor rubricae*, *Paralouatta varonai*, *Patasola magdalenae*, *Stirtonia tatacoensis*, *S. victoriae*, and *Xenothrix mcgregori*. Twelve most parsimonious trees (consensus in fig. 1A) are obtained with data set α, with conflicts within callitrichines plus *Lagonimico*, and within atelines. *C. carmenensis* appears as the sister group of (*Patasola-Callimico*). Three trees obtained with data set β suffer conflicts restricted to relationships within atelines (fig. 1B). *Branisella/Szalatavus* appears as the sister group of *Callimico*.

When both *Carlocebus carmenensis* and *Branisella/Szalatavus* are included, the number of trees increases to 60 and most resolution is lost with the computation of a strict consensus. In all of the trees, *C. carmenensis* remains in the same position: *C. carmenensis* is the sister group of (*Patasola-Callimico*); the same result obtains when *Branisella/Szalatavus* is excluded from the analysis. *Branisella/Szalatavus*, however, has five different positions in the trees: in some cases it is the sister of *Mohanamico*, the sister of (*Saimiri* ((*C. camenensis* (*Patasola, Callimico*)) (*Mohanamico* (*Lagonimico*, callitrichins)))), or basal to platyrrhines, catarrhines, or anthropoids. It is never among the ateloids.

Branisella/Szalatavus and *Carlocebus carmenensis* can be combined in a data set without substantial loss in resolution only if *Lagonimico*, *Patasola*, and *Mohanamico* and the other Patagonian taxa are excluded. The result is three most parsimonious trees, which differ only in the arrangement of the atelines (fig. 1C). *C. carmenensis* is the sister group of *Callimico*, and *Branisella/Szalatavus* is the sister group of (callitrichines, *C. carmenensis*, *Saimiri*). *Mohanamico* can be added and 48 trees are obtained and, in spite of the large number of topologies, variation is very localized. *Carlocebus carmenensis* adopts two different positions: it can be the sister group of either *Callimico* or of *Saimiri*. With the addition of other taxa to the data set, *Carlocebus carmenensis* appears within Ceboidea in most of the trials, in either the positions just described or more basal, but always above *Saimiri*, unless it appears at the bottom of the tree, as sister of anthropoids, of *Aegyptopitehcus*, or living anthropoids. *Branisella/Szalatavus* adopts many different positions relative to callitrichines, *Callimico*, *Mohanamico*, *Carlocebus*, and *Saimiri*. It is never located more basal than *Cebus* or within callitrichines. As with *Carlocebus carmenensis*, *Branisella/Szalatavus* may appear as low as sister group of anthropoids, for example when *Neosaimiri/Laventiana* or *Aotus dindensis* are added to the data set.

Patasola magdalenae occupies two positions, always deeply nested within the ceboids, depending on which other taxa are included in the analysis, unless the ceboids break up under addition of some combinations of Patagonian taxa (i.e., α plus *Homunculus* and *Dolichocebus* or β plus *Dolichocebus* alone or *Tremacebus* in addition). *Patasola* is either the sister group of *Callimico*, of callitrichines plus *Lagonimico*, or of callitrichines.

Lagonimico conclucatus usually has four alternative positions well nested within the Ceboidea: it is either the sister group of callitrichins (*Saguinus*, *Leontopithecus*, *Callithrix, Cebuella*), of the marmosets (*Callithrix* and *Cebuella*), or of *Aotus dindensis*, and this pair is the sister group of callitrichins, or finally, the sister group of the *Aotus-Mohanamico* pair (see below). It breaks away from these relationships when the whole clade Ceboidea breaks up, which occurs with certain combinations of α or β plus some Patagonian taxa (same examples as for *Patasola*).

Mohanamico hershkovitzi is always nested within the ceboids. It is most commonly the sister group of a clade composed of callitrichins plus *Lagonimico* and *Patasola* (data set α), which in some cases includes *Branisella/Szalatavus* (data set β). Although in some situations it is more basal, it is never below *Saimiri* and *Cebus* within Ceboidea. Only

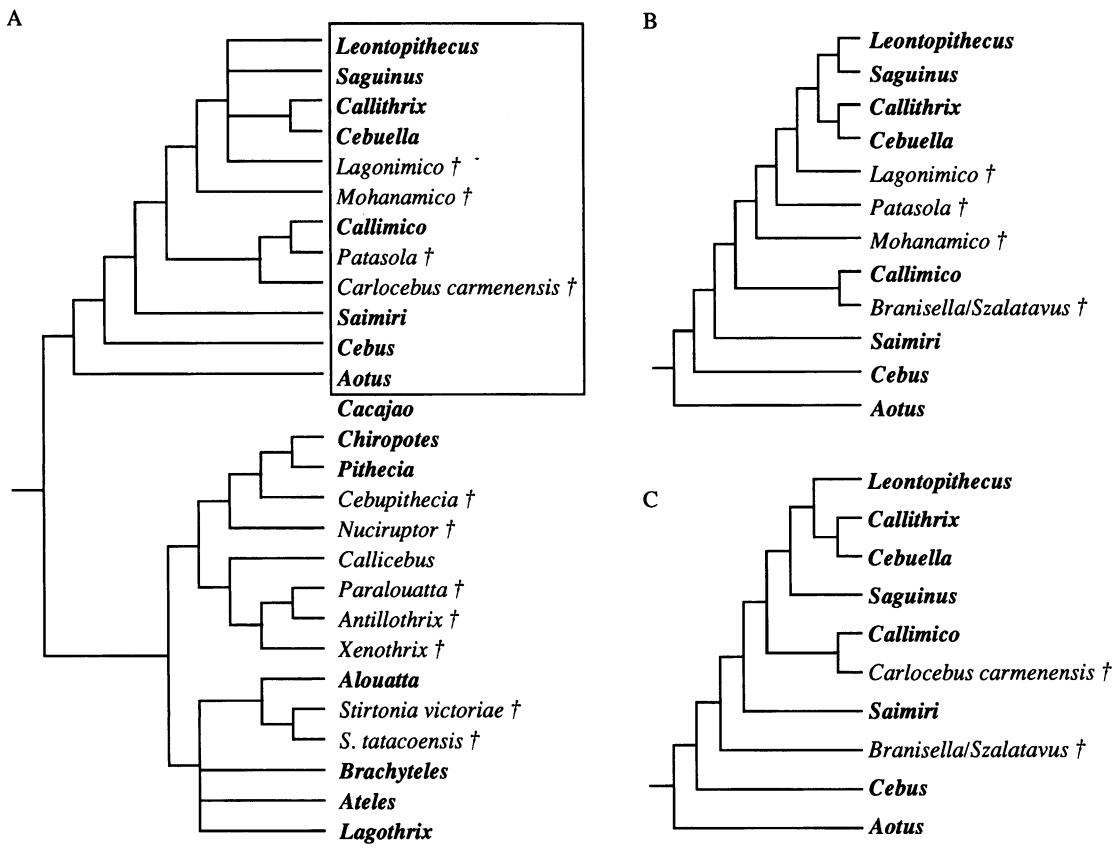

Fig. 1. Trees obtained with different combinations of taxa scored for morphological data (appendices 1 and 2). (A), (B), and (C) all agree on the topologies of the Ateloidea (not shown in the latter two). **(A)** Strict consensus of 12 most parsimonious trees trees (length = 299 steps, CI = 0.43, RI = 0.66) obtained with morphological characters for Recent platyrrhine genera and 10 fossil species, including *Carlocebus carmenensis* (data set α); **(B)** strict consensus of three most parsimonious trees trees (length = 295, CI = 0.43, RI = 0.66) obtained with morphological characters for Recent platyrrhine genera and 10 fossil species, including *Branisella boliviana/Szalatavus attricuspis* (data set β); and **(C)** strict consensus of three most parsimonious trees (length 287 steps, CI = 0.44, RI = 0.66) obtained with morphological characters including both *Carlocebus carmenensis* and *Branisella/Szalatavus* and excluding *Lagonimico conclucatus*, *Mohanamico hershkovitzi*, and *Patasola magdalenae*. "†" indicates fossil taxon.

when Ceboidea breaks up in the combinations described in the previous paragraph and a few others, such as β plus *Dolichocebus* and *Tremacebus* alone or if *Soriacebus* is added to the previous set, does *Mohanamico* not appear linked in these ways.

Three fossil genera have very stable positions: *Stirtonia victoriae* and *S. tatacoensis* are always sister taxa, and this clade in turn, is the sister group of *Alouatta*; *Cebupithecia* is always the sister group of pitheciins, with *Nuciruptor* the sister group of this clade. The only combination of taxa in which *Nuciruptor* breaks away from its group is with the α data set plus *Homunculus* and *Dolichocebus*.

Neosaimiri/Laventiana (pooled into a single terminal taxon) behaves in similar ways when combined with data set α or β. In both cases it is found among the basal taxa in three of the 12 most parsimonious trees (either as sister group of *Aegyptopithecus*, of living anthropoids, or of all anthropoids). In the remaining nine (in both α and β data sets), it is always located as the sister group

of the clade (*Saimiri* (*Patasola*, callitrichines)), to the exclusion of *Mohanamico*. *Branisella/Szalatavus* or *Carlocebus carmenensis*, *Cebus,* and *Aotus*, adopt unusual relationships among themselves: in these nine trees, *Cebus* and *Aotus* form a monophyletic group, and *Mohanamico* and *Branisella/Szalatavus* are either sister taxa, or either one is basal and the other sister of the crown group formed by *Neosaimiri/Laventiana*, etc. In the case of the α data set, *Carlocebus carmenensis* is driven to the bottom of all trees, as sister group of all anthropoids. The position of *Neosaimiri/Laventiana* in these nine trees (in both α and β data sets) drives a single position for *Lagonimico* as sister group of the *Callithrix/Cebuella* pair.

Aotus dindensis, in spite of its generic denomination, does not link with living *Aotus* in any analyses described herein. When it does not appear at the bottom of the tree, it always appears nested within ceboids, never among callitrichines. The positions of *Dolichocebus*, *Homunculus*, *Tremacebus*, both species of *Soriacebus*, and *Carlocebus intermedius* were evaluated in combination with both the α and β data sets; most resolution, however, was lost. *Soriacebus adrianae* and *S. ameghinorum* formed a clade in all trees, but *Carlocebus carmenensis* and *intermedius* did not. The Antillean clade is sister group of *Callicebus* in most trials, except in some of the trees generated under some combinations of Patagonian species in the α and β data sets (e.g., with α plus *Homunculus*, α plus *Homunculus* and *Dolichocebus*, β plus *Dolichocebus*, or β plus *Dolichocebus*, *Tremacebus*, *Soriacebus*, and *Homunculus*).

Effects of Addition of Fossils to Morphology-Based Trees

Addition of different fossil taxa to the Recent taxa data set has different effects on the preexisting trees depending on the fossil taxon in question and on the combination of taxa already included. Fossils either do not alter the number of most parsimonious trees, reduce it, or increase it. They either change the topology among the preexisting taxa, or they do not. Fossil taxa can either have stable positions or many different positions.

Data for Recent taxa only produce six most parsimonious trees, all with a stable ceboid grouping, but with different relationships among ceboids, pitheciins, *Callicebus*, and atelids. When *Cebupithecia* is added, a single tree is obtained, which (except for including *Cebupithecia*) is identical to one of the six including Recent taxa only.

Let us consider the α data set before addition of *Patasola*, *Lagonimico*, *Mohanamico*, and *Carlocebus carmenensis*: it forms three most parsimonious trees. When *Patasola* is added, the number of trees increases to 18. The number further increases to 84 with addition of *Mohanamico,* and decreases to 18 again with *Lagonimico*; the number of trees further decreases to 12 when one adds *C. carmenensis*. Addition of *Homunculus* raises the number of trees to 56, with *Tremacebus* the number of trees remains the same, increases to 372 with *Dolichocebus*, and decreases to 35 with *Soriacebus* (both species). Similarly, addition of fossils to the β data set produces oscillating numbers of trees. Addition of *Nuciruptor* to the *Cebupithecia* + Recent taxa tree, however, leaves the unique topology unaltered.

Some fossil taxa are associated with a particular taxon but when this taxon and/or other close relatives are deleted from the data set, the fossil taxon does not necessarily link with the next closest relative, but may associate with many different taxa because the driving characters become autapomorphies and other potentially informative characters are missing. For example, in the α data set, if one excludes *Callimico* and *Patasola*, one obtains 235 trees; *Carlocebus carmenensis* does not appear as a basal callitrichine but in many different positions in the tree, and topologies vary among the rest of the taxa as well.

Simultaneous Analysis of Morphological and Molecular Data

Positions of the Fossil Taxa

More fossils can be added to this data set than to the exclusively morphological one, without loss of resolution. The highest resolution, with a totally resolved single tree, is obtained when the following 18 fossil platyrrhine taxa are combined with the 16 Recent genera: *Antillothrix bernensis*, *Branisella bo-*

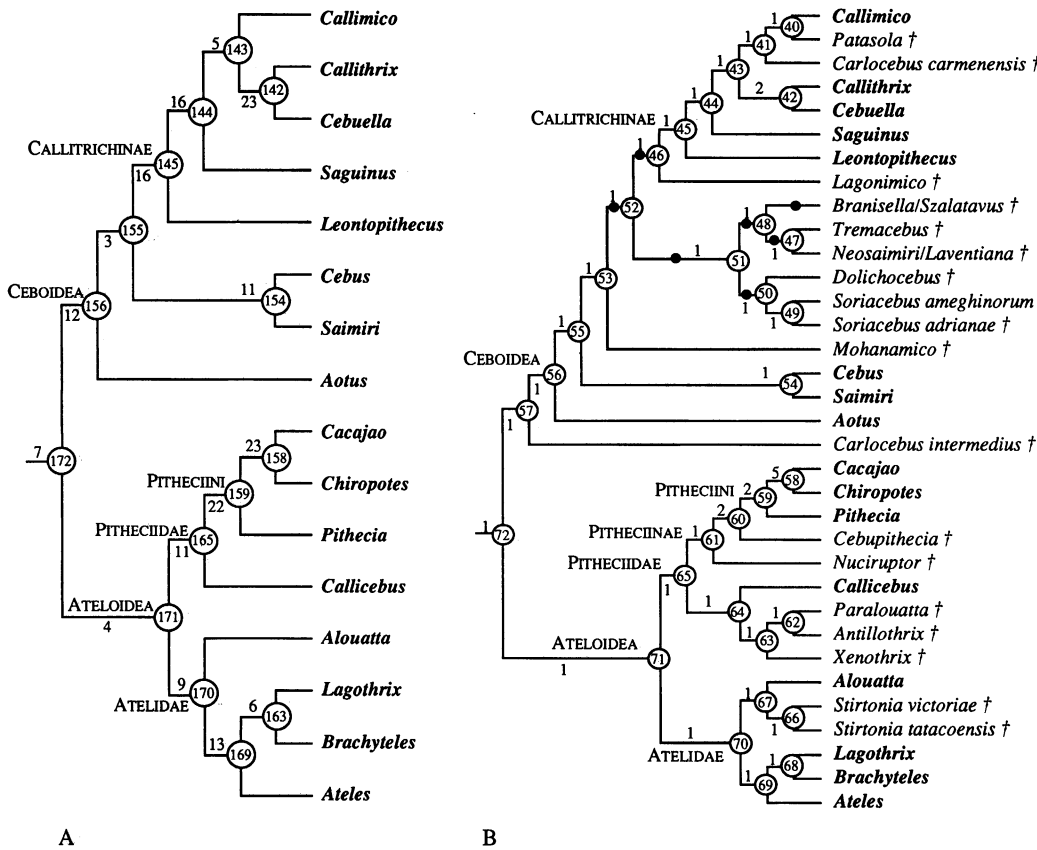

Fig. 2. Most parsimonious trees obtained with simultaneous analysis of morphological characters and nuclear (IRBP and ε-globins) and mitochondrial (12S and partial 16S) gene sequences for **(A)** Recent taxa only (one tree, length = 3,221 steps, CI = 0.52, and RI = 0.58) and **(B)** Recent plus fossil taxa (one tree, length = 3,303 steps, CI = 0.52, and RI = 0.58). The seven dots on the branches indicate the seven positions of *Aotus dindensis* in the seven most parsimonious trees obtained when this taxon was added to the data set. All other relationships remained the same in the seven trees. Numbers above or below branches show Bremer support values. Encircled numbers identify nodes. Morphological character support for each node is shown in tables 2A (for tree A) and 2B (for tree B). "†" indicates fossil taxon.

liviana/Szalatavus attricuspis, *Carlocebus carmenensis*, *Carlocebus intermedius*, *Cebupithecia sarmientoi*, *Dolichocebus gaimanensis*, *Lagonimico conclucatus*, *Mohanamico hershkovitzi*, *Neosaimiri fieldsi/Laventiana annectens*, *Nuciruptor rubricae*, *Paralouatta varonai*, *Patasola magdalenae*, *Soriacebus adrianae*, *Soriacebus ameghinorum*, *Stirtonia tatacoensis*, *Stirtonia victoriae*, *Tremacebus harringtoni,* and *Xenothrix mcgregori* (fig. 2B). With the addition of *Aotus dindensis*, seven trees are obtained, and this species is the only one that changes positions (fig. 2B). The relationships among the Recent taxa remain invariable and identical to the topology obtained excluding all fossil taxa (fig. 2A; see Horovitz, 1997; Horovitz and Meyer, 1997; Horovitz et al., 1998).

Branisella/Szalatavus appears as the sister species of the *Tremacebus-Neosaimiri/Laventiana* group; these three taxa are in turn the sister group of the Patagonian *Soriacebus-Dolichocebus* group. This entire clade, composed exclusively of fossil taxa, is the sister group of a clade where *Lagonimico* is basal to living callitrichines; in this clade *Leontopithecus* is the most basal, the next to branch

off is *Saguinus*, and finally, *Callithrix-Cebuella* are the sister group of ((*Callimico, Patasola*) *Carlocebus carmenensis*). *Mohanamico hershkovitzi* is the sister species of this clade, and further basal appear the pair *Cebus-Saimiri*, and finally living *Aotus*. This large clade which I will call Ceboidea is the sister group of a fossil species, *Carlocebus intermedius*. Another large clade, Ateloidea, is composed of Pitheciidae, that include the Antillean taxa plus *Callicebus*, as sister group of the Pitheciinae (*Nuciruptor* (*Cebupithecia,* pitheciins)). The pitheciins are *Pithecia*, *Chiropotes*, and *Cacajao*. Pitheciids are the sister group of the Atelidae, which includes the fossil *Stirtonia* species, associated with *Alouatta*, and this clade is the sister group of (*Ateles* (*Lagothrix*, *Brachyteles*)). When one adds *Aotus dindensis*, this species adopts seven different positions (fig. 2A): all of these positions are within Ceboidea, within or just above or below the clade composed exclusively of fossils. When *Homunculus* is added, it not only shows many different positions, but many other fossil taxa also move around; 1,238 was the total number of most parsimonious trees found; in the consensus tree, ceboids and ateloids collapse. The only clades that stay together in the strict consensus are: *Callithrix* and *Cebuella*, *Soriacebus ameghinorum* and *S. adrianae*, atelids, and pitheciines.

Relationships also change when fewer fossil taxa are included. When one excludes *Patasola* from the set of 18 fossil taxa, *Carlocebus carmenensis* does not associate with *Callimico* as one could expect, but with either *Neosaimiri/Laventiana* or next to basal in the all-fossil clade, with *Neosaimiri/Laventiana* as basal, and *Branisella/Szalatavus* sister group of *Callimico* in all four most parsimonious trees obtained. When *Branisella/Szalatavus* is excluded, *Carlocebus carmenensis* is either a member of the all-fossil clade (that is monophyletic in all nine most parsimonious trees) or the sister group of the *Patasola-Callimico* pair. When *Branisella/Szalatavus* and all Patagonian taxa except *Carlocebus carmenensis* and *intermedius* are excluded, seven most parsimonious trees obtain: *C. carmenensis* is either the sister group of *Callimico*, of *Neosaimiri/Laventiana* or the sister group of *Patasola* and *Callimico*. *Soriacebus*, *Dolichocebus*, *Tremacebus*; and *Neosaimiri/Laventiana* form the all-fossil clade when they are included in certain combinations or all at once; when included individually, a large number of trees is obtained and Ceboidea + *Carlocebus intermedius*, most nodes within, and ateloidea collapse in the strict consensus. In any combination tried, *Homunculus patagonicus* has highly variable positions.

Branisella/Szalatavus occupies different positions depending on the combination of fossils: it is the sister group of *Callimico* only if *Patasola* is excluded from the data set; when *Carlocebus carmenensis* is excluded, *Branisella/Szalatavus* is still within the all-fossil clade. *Patasola* is the sister group of *Callimico* in almost every trial. Many fossil taxa have to be excluded before *Patasola* changes positions, but it consistently remains within ceboids, above the branching of *Cebus-Saimiri*. *Lagonimico* appears as sister group of callitrichines, except when many fossil taxa are excluded; in some trials it may appear linked with (*Callithrix*, *Cebuella*) or with (*C. carmenensis* (*Patasola*, *Callimico*)). *Mohanamico* has a relatively stable position. Many taxa have to be excluded before it changes to a position other than that in the tree including 18 fossil taxa. The Antillean clade appears as a sister group of *Callicebus* in the great majority of trials, except when *Homunculus* is added or when the members of the all-fossil clade are included individually: then most clades collapse, including the Antillean clade.

Effects of Addition of Fossils to the Simultaneous Analysis of Morphological and Molecular Data

In no case did fossils modify the relationships among Recent taxa (which are the same as in trees where no fossils are included). Fossils can have a stable position or adopt many different ones, producing a large number of most parsimonious trees. Certain combinations of fossils produce many fewer trees than when included separately. For example, if the Patagonian *Tremacebus*, *Dolichocebus,* and *Soriacebus* are included individually, they link onto many different places on the trees, however when included together or in

certain paired combinations, they appear within Ceboidea. It seems that the reason for this is that fossil taxa present combinations of characters not found among living taxa. These characters appear in a mosaic fashion among the nodes; only when the picture is more complete does this mosaic pattern emerge and groups of fossils adopt stable positions on the tree.

Character Support for Fossil Taxa Affinities

The single tree obtained including the 18 fossils in the combined analysis (fig. 2B) was the best hypothesis of fossil taxa affinities in terms of completeness and resolution; therefore, a detailed account of unambiguous character support for different nodes connected to fossil taxa on this tree is given here. Tables 2A and 2B list character support for the trees based on Recent taxa only (fig. 2A) and Recent taxa plus fossils (fig. 2B): note that in addition to showing a higher number of nodes, table 2B shows a lower support for each one. Further details on character definitions can be found in Appendix 1 (see also Horovitz and MacPhee, 1999). Higher taxon names are those shown in figure 2B. A basal dichotomy of platyrrhines gives rise to two major clades, which are here called Ceboidea + *Carlocebus intermedius* and Ateloidea. Ceboidea is defined as the clade containing *Aotus* and *Callithrix* and all intermediate nodes and their descendants and Ateloidea as containing *Ateles*, *Pithecia*, and all intermediate nodes and their descendants.

Platyrrhini (node 72) is supported by four characters: presence of ossification in the tentorium cerebelli (ch. 13), presence of a canal connecting the subarcuate fossa and the sigmoid sinus (ch. 17), zygomatic-parietal contact in the pterion region (ch. 24), and M^3 and P^4 are subequal in length (ch. 78). Node 57, that links Ceboidea and *Carlocebus intermedius*, is supported by the presence of a vertex on C_1, on the mesial end of its lingual cingulum (ch. 38).

Ceboidea (node 56) is supported by a P_2 that is enlarged relative to the other premolars (ch. 42). Node 55 that includes *Cebus*, *Callithrix*, and all intermediate nodes and their descendants has no unambiguous morphological support (only molecular characters support it unambiguously). Node 53, which includes *Mohanamico*, *Callithrix*, and all intermediate nodes and their descendants, is supported by the enlargement of the P_3 protoconid from being subequal to larger than the P_4 protoconid (ch. 44) and loss of the hypoconid on P_4 (ch. 48). Node 52, which includes *Soriacebus*, *Callithrix*, and all the intermediate nodes and their descendants, is supported by the loss of the entoconid on P_4 (ch. 49). Node 46, which includes *Lagonimico*, *Callithrix*, and all the intermediate nodes and their descendants, is supported by the presence of a buccal cingulum on $M_{1,2}$ (ch. 55), loss of hypocone on M^1 (ch. 72) and M^2 (ch. 76), and a reduced buccal cingulum (ch. 81). Callitrichinae (Node 45) is supported by loss of M_3^3's (ch. 58 and 78). Node 44 (*Saguinus*, *Callithrix*, etc.) is not supported by any unambiguous morphological characters (only molecular). Node 43 (*Callithrix*, *Callimico*, etc.) receives no morphological support at all (only molecular). Node 41 (*Carlocebus*, *Patasola*, and *Callimico*) is supported by gain of hypocone and prehypocrista on M^1 (ch. 72), gain of hypocone on M^2 (ch. 76), and widening of buccal cingulum on M_1 (ch. 81); node 40 (*Callimico* and *Patasola*) is supported by a lingual displacement of the hypocone on M^1 (ch. 74).

Node 51 is composed exclusively of fossil taxa (*Soriacebus*, *Tremacebus*, etc.) and is supported by the gain of a hypocone on P^4 (ch. 69); node 50 (*Soriacebus* and *Dolichocebus*) by the loss of the vertex on the C_1 lingual cingulum mesial end (ch. 38), gain of a prehypocrista on M^1 (ch. 72), and gain of a prominence on the P^2 buccal wall (ch. 85); *Soriacebus ameghinorum* and *adrianae* (node 49) by the presence of a bulging surface on the buccal wall of C_1 (ch. 83); node 48 (*Branisella/Szalatavus*, *Tremacebus*, and *Neosaimiri/Laventiana*) by gain of a mesostyle on M^1 (ch. 71); and finally, node 47 (*Tremacebus* and *Neosaimiri/Laventiana*) is supported by a reorientation of the oblique cristid that intersects the protolophid lingually to the protoconid (ch. 52).

Ateloidea (node 71) is supported by the presence of a shallow pterygoid fossa (ch. 16) and a deciduous P_2 that has a rounded

cross section (ch. 41); Pitheciidae (node 65) by a trigonid and talonid that have subequal heights (ch. 56) and gain of a prehypocrista on M^1 (ch. 72); Pitheciinae (node 61) by styliform $I_{1,2}$ (ch. 31) and a lingual cingulum on C_1 that is not elevated mesially (ch. 37); node 60 (*Cebupithecia*, Pitheciini) by the presence of a diastema between C_1 and I_2 (ch. 33) and a wedge-shaped C_1 with a sharp ligual edge (ch. 36). Node 64 (*Callicebus* and Antillean clade) is supported by presence of paired prominences on the cochlear housing lateral wall (ch. 15), a zygomatic arch that extends lower than the alveolar level (ch. 23), a C_1 that has a highly compressed root (ch. 34), and a C^1 alveolus that is smaller than that of P^4 (ch. 62); the Antillean clade (node 63) by a wide nasal fossa (ch. 25), a C_1 alveolus that is buccolingually smaller than that of P_4 (ch. 39), and presence of a bulging buccal wall on M_1 at the level of the protoconid (ch. 53); and node 62 (*Paralouatta* and *Antillothrix*) by six characters: oblique cristid intersects the protolophid lingual to the protoconid (ch. 52), the lingual cingulum projects mesially (ch. 68), the P^4 is subequal to M^1 in width (ch. 70), the M^1 has a distinct pericone (ch. 73), the M^1 postmetacrista has a distobuccal slope (ch. 74), and the M^1 hypocone is lingually located with respect to the protocone (ch. 75).

Atelidae (node 70) is supported by six characters: reduction in the number of lumbar vertebrae (ch. 2), presence of a ventral glabrous surface on the tail (ch. 5), enlargement of the temporal emissary foramen (ch. 20), enlargement of the P_2 relative to other premolars (ch. 42), position of the protocone mesial to the widest point on the trigon (ch. 66), and loss of the lingual cingulum on P^4 (ch. 67); node 67 (*Alouatta* and *Stirtonia*) by the projecting distobuccal quadrant of the M_1 (ch. 51), reorientation of the oblique cristid on the M_1, which intersects the protolophid lingual to the protoconid apex (ch. 52), presence of a mesoloph on M^1 (ch. 71), and a widening of the talonid (ch. 82); finally, *Stirtonia tataconesis* and *S. victoriae* (node 66) is supported by the presence of parastyles on M^1 (ch. 79).

DISCUSSION

Incompatible Taxa

In both sets of trials, morphological and simultaneous analysis of morphological and molecular data, pairs of taxa were identified that seem to be "incompatible" under certain circumstances. Two taxa are "incompatible" when one of the two is included in separate analyses to the exclusion of the other, few trees and a high resolution in the consensus are generated, but when combined, the outcome is a large number of trees with low resolution in the consensus and usually one of the "incompatible" taxa appearing at the bottom of the tree. This may be overcome if certain other taxa are deleted or added in the combined analysis. For example, in the morphology-only analysis, *Carlocebus carmenensis* and *Branisella/Szalatavus* are incompatible and can only be combined if *Mohanamico*, *Lagonimico*, and *Patasola* are excluded.

With the morphological data set, *Branisella/Szalatavus* has a stable position as sister group of *Callimico* when *Carlocebus* is excluded. When *Carlocebus* is also included, however, it links with *Callimico* and *Patasola* whereas *Branisella/Szalatavus* and *Callimico* do not pair up anymore: *Carlocebus* and *Branisella/Szalatavus* are incompatible as sister taxa of *Callimico* and *Patasola* because one unambiguous and one ambiguous character they share with them are different. For example, the presence of a mesostyle supports a sister-group relationship between *Callimico* and *Branisella/Szalatavus*, whereas this character is absent in *Carlocebus*, and the monophyly of *Carlocebus-Patasola-Callimico* is supported by a oblique cristid on M_1 that intersects the protolophid in a position lingual to the protoconid, different from *Branisella/Szalatavus*.

Fossils as Links

The number of trees decreases from six to one with addition of *Cebupithecia* to the morphological data set including Recent taxa only; this is due to the fact that this fossil presents a combination of characters that is intermediate between *Callicebus* and pitheciins. When one excludes *Cebupithecia* from the analysis, the affinities of pitheciins are ambiguous. Some characters are synapomorphic in *Cebupithecia* and pitheciins (i.e., canines with a sharp lingual edge, procumbent upper incisors), but another one (smooth

TABLE 2

Characters Supporting Nodes from Trees on Figure 2

Tree on figure 2A			Tree on figure 2B		
Branch	Character	Change	Branch	Character	Change
External node → 172	13. Tentorium ossification	0 ⇒ 1	External node → 72	13. Tentorium ossification	0 ⇒ 1
	17. Canal subarcuate fossa	0 ⇒ 1		17. Canal subarcuate fossa	0 ⇒ 1
	24. Pterion region contact	1 ⇒ 0		24. Pterion region contact	1 ⇒ 0
	78. M^3/P^4 length	3 ⇒ 2		78. M^3/P^4 length	3 ⇒ 2
172 → 156	54. M_1 entoconid position	1 ⇒ 0	72 → 57	38. C_1 lingual cingulum vertex	0 ⇒ 1
	58. M_3/P_4 length	3 ⇒ 2	57 → 56	42. P_2 size	0 ⇒ 1
	60. I^1 lingual heel	1 ⇒ 0			
	78. M^3/P^4 length	2 ⇒ 1			
156 → 155	58. M_3/P_4 length	2 ⇒ 1	56 → 55	No unambiguous morphological support	
155 → 145	1. Number of offspring	0 ⇒ 1	55 → 53	44. P_3/P_4 protoconid size	0 ⇒ 1
	6. Claws	0 ⇒ 1		48. P_4 hypoconid	1 ⇒ 0
	16. Pterygoid fossa	0 ⇒ 1	53 → 52	49. P_4 entoconid	1 ⇒ 0
	22. Cranial capacity	1 ⇒ 0	52 → 46	55. $M_{1,2}$ buccal cingulum	0 ⇒ 1
	44. P_3/P_4 protoconid size	0 ⇒ 1		72. M^1 hypocone/prehypocrista	1 ⇒ 2
	48. P_4 hypoconid	1 ⇒ 0		76. M^2 hypocone presence	1 ⇒ 0
	49. P_4 entoconid	1 ⇒ 0		81. M_1 buccal cingulum width	1 ⇒ 0
	58. M_3/P_4 length	1 ⇒ 0	46 → 45	58. M_3/P_4 length	3 ⇒ 0
	72. M^1 hypocone/prehypocrista	1 ⇒ 2		78. M^3/P^4 length	1 ⇒ 0
	76. M^2 hypocone presence	1 ⇒ 0			
	78. M^3/P^4 length	1 ⇒ 0			
	81. M_1 buccal cingulum width	1 ⇒ 0			
145 → 144	No unambiguous morphological support		45 → 44	No unambiguous morphological support	
144 → 143	No morphological support		44 → 43	No morphological support	
			43 → 41	72. M^1 hypocone/prehypocrista	2 ⇒ 0
				76. M^2 hypocone presence	0 ⇒ 1
				81. M_1 buccal cingulum width	0 ⇒ 1
			41 → 40	74. M^1 protocone/hypocone	0 ⇒ 1

TABLE 2—(*Continued*)

Tree on figure 2A			Tree on figure 2B		
Branch	Character	Change	Branch	Character	Change
143 → Callimico	1. Number of offspring	1 ⇒ 0	40 → Callimico	46. P_3 Metaconid height	1 ⇒ 2
	12. Postglenoid foramen	2 ⇒ 1		51. M_1 distobuccal projection	0 ⇒ 1
	16. Pterygoid fossa	1 ⇒ 0		55. $M_{1,2}$ buccal cingulum	1 ⇒ 0
	27. Zygomaticofacial foramen	0 ⇒ 1		71. M^1 mesostyle	0 ⇒ 1
	44. P_3/P_4 protoconid size	1 ⇒ 0			
	51. M_1 distobuccal projection	0 ⇒ 1			
	55. $M_{1,2}$ buccal cingulum	1 ⇒ 0			
	58. M_3/P_4 length	0 ⇒ 1			
	72. M^1 hypocone/prehypocrista	2 ⇒ 0			
	76. M^2 hypocone presence	0 ⇒ 1			
	78. M^3/P^4 length	0 ⇒ 1			
143 → 142	14. Pneumatized middle ear	0 ⇒ 1	43 → 42	28. dI_2 shape	1 ⇒ 0
	28. dI_2 shape	1 ⇒ 0		29. I_1/I_2 height	2 ⇒ 1
	29. I_1/I_2 height	2 ⇒ 1		30. I_1/I_2 alignment	0 ⇒ 1
	30. I_1/I_2 alignment	0 ⇒ 1		31. $I_{1,2}$ shape	0 ⇒ 1
	31. $I_{1,2}$ shape	0 ⇒ 1		32. Meso/and distostyles of $I_{1,2}$	0 ⇒ 1
	32. Meso-and distostyles of $I_{1,2}$	0 ⇒ 1		34. C_1 root shape	0 ⇒ 1
	34. C_1 root shape	0 ⇒ 1		35. C_1 lingual cingulum	1 ⇒ 0
	35. C_1 lingual cingulum	1 ⇒ 0		38. C_1 lingual cingulum vertex	1 ⇒ 0
	38. C_1 lingual cingulum vertex	1 ⇒ 0		45. P_3/P_2 talonid	0 ⇒ 1
	45. P_3/P_2 talonid	0 ⇒ 1		47. P_4 meta/protoconid height	1 ⇒ 0
	47. P_4 meta/protoconid height	1 ⇒ 0		63. dP^2 trigon	1 ⇒ 0
	63. dP^2 trigon	1 ⇒ 0		83. C_1 buccal prominence	0 ⇒ 1
	83. C_1 buccal prominence	0 ⇒ 1	52 → 51	69. P^4 hypocone	0 ⇒ 1
			51 → 48	71. M^1 mesostyle	0 ⇒ 1
			48 → 47	52. M_1 oblique cristid orientation	0 ⇒ 1
			51 → 50	38. C_1 lingual cingulum vertex	1 ⇒ 0
				72. M^1 hypocone/prehypocrista	1 ⇒ 0
				85. P_2 buccal prominence	0 ⇒ 1
			50 → 49	83. C_1 buccal prominence	0 ⇒ 1
155 → 154	18. Vomer exposure in orbit	0 ⇒ 1	55 → 54	18. Vomer exposure in orbit	0 ⇒ 1
	70. P^4/M^1 buccolingual breadth	0 ⇒ 1		58. M_3/P_4 length	2 ⇒ 1
				70. P^4/M^1 buccolingual breadth	0 ⇒ 1

TABLE 2—*(Continued)*

Tree on figure 2A			Tree on figure 2B		
Branch	Character	Change	Branch	Character	Change
172 → 171	16. Pterygoid fossa depth	0 ⇒ 1	72 → 71	16. Pterygoid fossa depth	0 ⇒ 1
	41. dP_2 cross section shape	1 ⇒ 0		41. dP_2 cross section shape	1 ⇒ 0
	69. P^4 hypocone	0 ⇒ 1			
171 → 165	56. M_2 trigonid/talonid height	0 ⇒ 1	71 → 65	56. M_2 trigonid/talonid height	0 ⇒ 1
				72. M^1 hypocone/prehypocrista	1 ⇒ 0
165 → 159	28. dI_2 shape	1 ⇒ 2	65 → 61	31. $I_{1,2}$ shape	0 ⇒ 1
	31. $I_{1,2}$ shape	0 ⇒ 1		37. C_1 lingual cingulum elevated	1 ⇒ 0
	33. Diastema between C_1 and I_2	0 ⇒ 1	61 → 60	33. Diastema between C_1 and I_2	0 ⇒ 1
	36. C_1 lingual crest sharpness	0 ⇒ 1		36. C_1 lingual crest sharpness	0 ⇒ 1
	37. C_1 lingual cingulum elevated	1 ⇒ 0	60 → 59	59. Molar enamel surface	0 ⇒ 1
	57. M_2 mesoconid	0 ⇒ 1		67. P^4 lingual cingulum	1 ⇒ 0
	58. M_3/P_4 length	3 ⇒ 2			
	59. Molar enamel surface	0 ⇒ 1			
	61. I^2 orientation	0 ⇒ 1			
	65. P^3 preparacrista	0 ⇒ 1			
159 → 158	70. P^4/M^1 buccolingual breadth	0 ⇒ 1	59 → 58	70. P^4/M^1 buccolingual breadth	0 ⇒ 1
				72. M^1 hypocone/prehypocrista	0 ⇒ 1
			65 → 64	15. Middle ear paired prominences	0 ⇒ 1
				23. Zygomatic arch ventral extent	1 ⇒ 0
				34. C_1 root shape	0 ⇒ 1
				62. C^1/P^4 alveolus size	0 ⇒ 1
			64 → 63	25. Nasal fossa width	0 ⇒ 1
				39. C_1/P_4 alveolus size	0 ⇒ 1
				53. M_1 bulging protoconid	0 ⇒ 1
			63 → 62	52. M_1 oblique cristid orientation	0 ⇒ 1
				68. P^4 lingual cingulum projected	0 ⇒ 1
				70. P^4/M^1 buccolingual breadth	0 ⇒ 1
				73. M^1 postmetacrista slope	1 ⇒ 0
				74. M^1 protocone/hypocone	0 ⇒ 1
				75. M^1 pericone/lingual cingulum	1 ⇒ 2

TABLE 2—*(Continued)*

Tree on figure 2A			Tree on figure 2B		
Branch	Character	Change	Branch	Character	Change
171 → 170	2. Number of lumbar vertebrae	0 ⇒ 1	71 → 70	2. Number of lumbar vertebrae	0 ⇒ 1
	5. Tail ventral glabrous surface	0 ⇒ 1		5. Tail ventral glabrous surface	0 ⇒ 1
	20. Temporal emissary foramen	1 ⇒ 0		20. Temporal emissary foramen	1 ⇒ 0
	66. P^4 protocone position	1 ⇒ 0		42. P_2 size	0 ⇒ 1
				66. P^4 protocone position	1 ⇒ 0
				67. P^4 lingual cingulum	1 ⇒ 0
170 → 169	No unambiguous morphological support		70 → 67	51. M_1 distobuccal projection	0 ⇒ 1
				52. M_1 oblique cristid orientation	0 ⇒ 1
				71. M^1 mesostyle	0 ⇒ 2
				82. M_1 talonid/trigonid width	0 ⇒ 1
			67 → 66	79. M's parastyles	0 ⇒ 1
			70 → 69	75. M^1 pericone/lingual cingulum	1 ⇒ 0
175 → 174	7. Carpometacarpal joint	0 ⇒ 1	75 → 74	7. Carpometacarpal joint	0 ⇒ 1
	12. Postglenoid foramen	1 ⇒ 0		12. Postglenoid foramen	1 ⇒ 0
	19. Ectotympanic shape	1 ⇒ 0		19. Ectotympanic shape	1 ⇒ 0
				67. P^4 lingual cingulum	1 ⇒ 0
174 → 173	4. External tail	1 ⇒ 0	74 → 73	4. External tail	1 ⇒ 0
	8. Rib cage shape	0 ⇒ 1		8. Rib cage shape	0 ⇒ 1
	9. Ulnar participation in wrist	0 ⇒ 1		9. Ulnar participation in wrist	0 ⇒ 1
	10. Sternebral proportions	0 ⇒ 1		10. Sternebral proportions	0 ⇒ 1

molar enamel), that is derived in pitheciins is plesiomorphic in *Cebupithecia*. Therefore *Cebupithecia* acts as a link between *Callicebus* and pitheciins. Pitheciins possess such a comparatively large array of apomorphic states, that when *Cebupithecia* is excluded, it is hard to establish any particular affinity with other platyrrhines, and several different possibilities arise as equally parsimonious.

Morphological Versus Simultaneous Analysis

The simultaneous analysis in general allows for inclusion of more fossils than the morphological analysis, maintaining a high resolution. When the same combination of taxa for which seven trees obtain in the combined analysis is run with morphological characters only, 79 trees obtain. I have identified one factor that may be contributing to this interesting effect: the morphology-only data set allows for variation in relationships among Recent taxa when different sets of fossils are included. The combined data set rules out this variation: relationships among Recent taxa remain unaltered no matter how many or in what combinations the fossil taxa are added. This strength of the combined data set could be the result of the phylogenetic signal common to all data sets adding up, overcoming individual homoplasies. All that is left to vary in the combined analysis are the positions of the fossil taxa themselves. Given the topology imposed by the combined data set on the Recent taxa, fossils do not seem to have that many parsimonious alternative positions, except the case of *Homunculus patagonicus*, which has an unusual combination of characters, and may actually represent more than one taxon.

Old and New Hypotheses of Fossil Platyrrhine Affinities

Branisella boliviana/Szalatavus attricuspis is placed within ceboids closer to callitrichines than any living platyrrhines, which is compatible with the hypothesis of Takai and Anaya (1996). The combined analysis places *Branisella/Szalatavus* within the clade composed exclusively of fossil taxa, which is the sister group of the clade composed of callitrichines and *Lagonimico* (fig. 2B).

The position of the Patagonian taxa has always been elusive (see above). Even in this analysis, most of them are unstable, except for *Carlocebus carmenensis*, which appears within ceboids consistently in both morphological and combined analyses. *Soriacebus* is probably the Patagonian taxon that has been most forcibly argued to be a relative of the pitheciines (Rosenberger et al., 1990). The combined analysis, however, places it within ceboids as a member of the all-fossil clade that is supported, among other characters, by presence of a P_3 protoconid that is larger than its equivalent on P_4 (ch. 44), and by the absence of hypoconid and entoconid on P_4 (ch. 48 and 49). The association of *Dolichocebus* with *Soriacebus* is supported by characters that were scored on dental remains that have been tentatively referred to *Dolichocebus*, none of which could be scored on the type specimen. This result, however, is the best solution with the information available. The case of *Tremacebus* in relation to *Neosaimiri/Laventiana* is similar. *Homunculus patagonicus* as treated here may represent more than one taxon and its phylogenetic position is indeterminate.

Patasola magdalenae and *Lagonimico conclucatus* had been placed in the same position in two independent studies (Kay, 1994; Kay and Meldrum, 1997), but they had never been included in an analysis simultaneously. In those studies, based on morphological characters, *Callimico* was placed basal to callitrichines, and both *Patasola* and *Lagonimico* were intermediates between *Callimico* and the rest of callitrichines, or alternatively, *Patasola* was the sister group of *(Callithrix/Cebuella, Saguinus)*. In the present morphological analysis, the relationships inferred coincide with the previous hypothesis to a certain degree: in some of the trees, they adopt the predicted position between *Callimico* and the other callitrichines. In the combined data set tree, however, their positions are different (fig. 2B): *Callimico* is the closest living relative of *Callithrix-Cebuella*, and *Patasola* is the fossil sister group of *Callimico*. The position of *Patasola* as sister group of *Callimico* is also a common solution when molecular data is excluded, and seems therefore to be well supported. *Lagonimico* appears as the

sister group of callitrichines in the simultaneous analysis.

Of the hypotheses previously suggested for *Mohanamico hershkovitzi* (Luchterhand et al., 1986; Rosenberger et al., 1990; Kay, 1990; Kay and Meldrum, 1997), two of them are replicated in the morphological analysis presented here: these are an association of *Mohanamico* with callitrichines or with *Aotus dindensis*. The latter was obtained as one of many solutions when *Aotus dindensis* was included. In the combined analysis, *Mohanamico* is still among the ceboids, but in a more basal position, branching off a node higher than *Cebus-Saimiri*, and not associating with *Aotus dindensis*.

Two fossil genera, *Stirtonia* and *Cebupithecia*, were consistently associated with *Alouatta* and the pitheciins, respectively. These are historically the most accepted hypotheses. *Nuciruptor* is another stable taxon, and appears consistently associated with *Cebupithecia* + Pitheciini.

Neosaimiri fieldsi/Laventiana annectens does link in some cases with *Saimiri*, as previously suggested, but only when the morphological data set is analyzed under certain combinations of fossil taxa. In the simultaneous analysis, it is still a ceboid, but with *Branisella/Szalatavus* and most Patagonian taxa, it is a member of the clade composed exclusively of fossil taxa. Several differences with *Saimiri* (and, in some cases, with *Cebus*) prevent it from having a stable association with *Saimiri*. Some of these differences are as follows: in *Neosaimiri/Laventina* the protoconid of P_3 is larger than the metaconid and larger even than the protoconid of P_4, while in *Saimiri* it is subequal to the other two cusps; in *Neosaimiri/Laventiana* the P_3 talonid is subequal to that of P_2, while in *Saimiri* it is larger; the hypoconid on P_4 is absent in *Neosaimiri/Laventina* but present in *Saimiri*; there is a hypocone on P^4 in the fossils but none in *Saimiri*; and the P^4 is buccolingually narrower than M^1 in the fossils but subequal or larger in *Saimiri*.

Aotus dindensis was one of the most ubiquitous taxa within ceboids. It did not link with living *Aotus* in any of the analyses, even though *Aotus dindensis* and living *Aotus* were the only anthropoid taxa with a dorsoventrally compressed zygomatic arch (ch. 84; see Setoguchi and Rosenberger, 1987), which (at least in living *Aotus*) is due to a very enlarged orbit, in such a way that the zygomatic arch constitutes part of the front limit of the inferior orbital fissure. In spite of this character, there are differences between the two that suggest they do not share a common ancestor. The fossil species shows an enlarged protoconid on P_3, larger than the metaconid of the same tooth, and even larger than the protoconid on P_4, whereas in living species the protoconid and metaconid of P_3 are subequal as well as the protoconids of P_3 and P_4; the fossil lacks an entoconid on P_4 whereas living species possess one; in the fossil M_3 is mesiodistally longer than P_4, while in living *Aotus* these teeth are subequal in length. In the morphological and the simultaneous analyses, *Aotus dindensis* is always located above the branching of *Cebus-Saimiri*, and below callitrichines.

Carlocebus intermedius has a very unstable position in the morphological analyses. In the simultaneous analysis it does not link with *C. carmenensis* but appears as the sister group of ceboids (fig. 2B). Although there are no recorded differences between the two, there are no shared derived characters to link them either: their similarity is based on primitive characters. Only one character that is recorded for *C. intermedius* is unrecorded for *C. carmenensis*: the relative size of the P_2. In *C. intermedius* P_2 is the smallest lower premolar. As a test to evaluate whether they do link or not in the hypothetical case wherein *C. carmenensis* shows this same condition, the question mark for *C. carmenensis* in character 42 was replaced by "0." This data set was subject to a heuristic search, and two most parsimonious trees were obtained (same taxa shown in figure 2B, excluding *A. dindensis*): one topology was the same as in figure 2B, and the second showed *C. carmenensis* and *C. intermedius* as sister taxa, placed as the sister group of *Patasola-Callimico*, and all other aspects of the tree remained the same. Because of this lack of relevant information, it does not seem advisable to revise the systematics of the genus before more remains become available.

Implications for the Ages of Cladogenetic Events

The ages of the fossils included in the cladogram shown in figure 2B provide min-

imum ages for cladogenetic events. The oldest fossils are *Branisella boliviana* and *Szalatavus attricuspis*, of an age between 25.82 and 27.02 Ma, and they set the minimum age for the origin of node 51, its sister group, node 46, and all the more basal cladogenetic events, including the origin of Platyrrhini. At the very least these groups already existed at the age of *Branisella* and *Szalatavus*. The position of *Carlocebus carmenensis* is a surprising result; according to its age and very nested position within Ceboidea as sister group *Patasola* and *Callimico*, the stem lineage of *Callithrix* and *Cebuella*, *Saguinus*, *Leontopithecus*, and *Lagonimico* had already appeared in South America by the early Miocene. One should, however, consider that this position of *Carlocebus* in the phylogeny is rather unstable, and any conclusions derived from it very tentative.

Within the ateloids, the oldest fossils are *Stirtonia*, *Cebupithecia*, and *Nuciruptor* from the middle Miocene, which determines that the stem lineage of *Callicebus*-Antillean clade, stem lineage of pitheciins, *Alouatta*, and stem lineage of atelins, were in existence at that time.

Contribution of Fossils to Our Understanding of Character Evolution

There are advantages to the inclusion of fossils in a phylogenetic analysis; they frequently improve our understanding of character evolution in a group. One should bear in mind, however, that at the same time, fossils entail problems associated with incomplete preservation; for example, missing entries render characters optimizations ambiguous under some topologies.

Since the relationships among Recent taxa are identical in the trees generated with the simultaneous analysis including and excluding the fossil taxa (fig. 2A and B), it is possible to make direct comparisons of character evolution between the two. Fossils introduce intermediate nodes between Recent taxa. In some cases, this introduces a stepwise appearance of different characters along the phylogeny, that would seem to appear in larger clusters of synapomorphies in the phylogeny composed of Recent taxa only. If the characters can be scored in the fossil taxa and they are unambiguous, fossils introduce valuable information. The contrast between the stepwise appearance of characters and their appearance as cohesive complexes may be relevant to our understanding of the evolution of their functions (see Rae, 1997, for similar conclusions).

Three cases in which fossils are adding nodes between two Recent taxon nodes or between a node and a Recent terminal taxon demonstrate this phenomenon. The characters discussed are only those that are unambiguous in both phylogenies, the one including fossils (fig. 2B) and the one not including them (fig. 2A). The cases are: (1) transition from node 55 to Callitrichinae (node 45), with three intermediate steps in the tree including fossils: node 55 → node 53 → node 52 → node 46 → Callitrichinae (node 45); (2) transition from Pitheciidae (node 65) to Pitheciini (node 59), with two intermediate nodes, nodes 61 and 60; and (3) transition from node 43 to *Callimico*, with two intermediate nodes: node 43 → node 41 → node 40 → *Callimico*. Several characters are unambiguous in both cladograms (with or without fossils) and change along corresponding branches in both phylogenies.

Callitrichinae (node 145) in the Recent taxa cladogram is supported by the following characters (fig. 3A, table 2A): enlargement of the protoconid in P_3 in such a way that it is larger than that of the P_4, from a primitive condition in which the protoconids of both premolars are subequal (ch. 44); loss of hypoconid on P_4 (ch. 48); loss of entoconid on P_4 (ch. 49); loss of hypocone in M^1 and M^2 (ch. 72 and 76); M_3/M^3 absent (ch. 58 and 78); and reduced buccolingual width of buccal cingulum on M_1 talonid (ch. 81). The tree including the fossils shows that these characters evolved in four different cladogenetic events (fig. 3B). The first, leading from node 55 to node 53, involves characters 44 and 48; the second, with the origin of node 52, involves character 49; the third, leading to node 46, characters 72, 76, and 81; and the fourth, with the origin of Callitrichinae (node 45), characters 58 and 78.

The origin of Pitheciini (node 159; fig. 4A) is supported by presence of styliform permanent lower incisors (ch. 31); a diastema between C_1 and I_2 (ch. 33); presence of

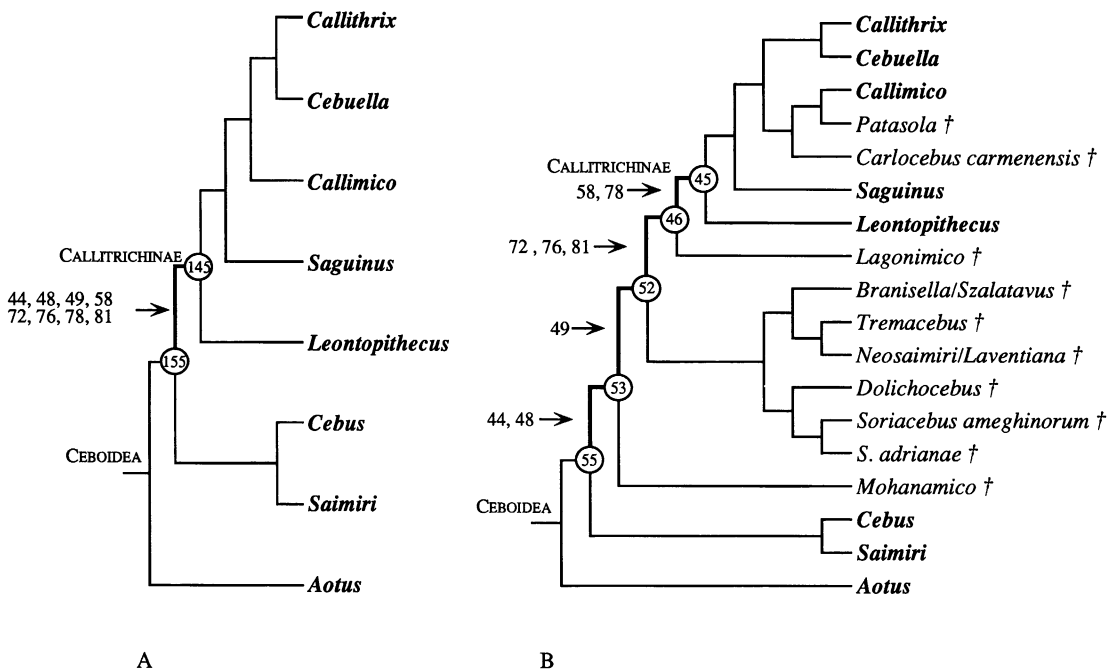

Fig. 3. **(A)** Characters supporting Callitrichinae (node 145) in the tree obtained with Recent taxa only, compared with **(B)** stepwise origin of the same characters when fossil taxa are added to the data set.

wedge-shaped lower canines with sharp edges on their lingual side (ch.36); C_1 lingual cingulum showing no mesial elevation (ch. 37); and molar enamel crenulated (ch. 59). Inclusion of *Cebupithecia* and *Nuciruptor* in the data set (fig. 4B) shows that these characters evolved in three steps and not as a complex: characters 31 and 37 appeared with the origin of Pitheciinae (node 61); characters 33 and 36 appeared with the origin of node 60; and character 59 turns out to be the only unambiguous one supporting Pitheciini (node 59), of those characters that were supporting it in figure 4A.

Callimico is an interesting taxon in the combined data set because it represents a re-

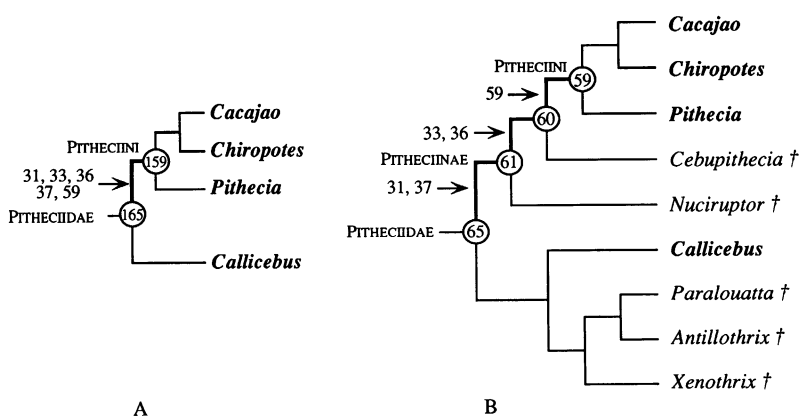

Fig. 4. **(A)** Characters supporting Pitheciini (node 159) in the tree obtained with Recent taxa only, compared with **(B)** stepwise origin of the same characters when fossil taxa are added to the data set.

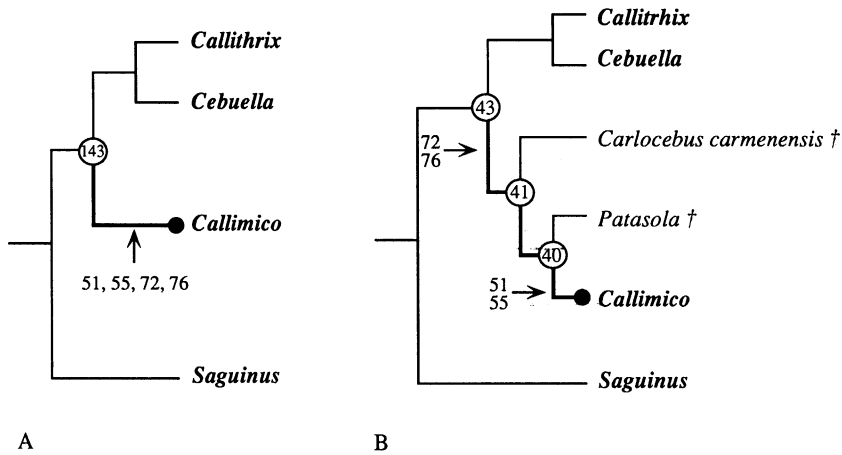

Fig. 5. **(A)** *Callimico* autapomorphies in the tree obtained with Recent taxa only, compared with **(B)** stepwise origin of the same characters when fossil taxa are added to the tree.

versal of several characters present in *Leontopithecus*, *Saguinus*, *Callithrix*, and *Cebuella*. Therefore, the two fossil taxa, *Carlocebus carmenensis* and *Patasola magdalenae* (though the former is not as stable in this position), that branch off in sequence between node 43 and *Callimico* are potentially valuable in analyzing the evolution of such reversals. Unfortunately, most of the characters that suffered reversals are not documented in the fossils; only two of them (ch. 72 and 76) are reversals and they both happen in the transition from node 43 to 41. Autapomorphies of *Callimico* in the tree with Recent taxa only (fig. 5A), include regain of a hypocone on M^1 (ch. 72); presence of a hypocone on M^2 (ch. 76); projecting distobuccal quadrant in M_1 (ch. 51); and presence of buccal cingulum in $M_{1,2}$ (ch. 55). The first two occur in the transition from node 43 to node 41, and the last two characters from node 40 to *Callimico* (fig. 5B).

In the first case, in the evolution from node 53 to Callitrichinae (node 45), the intermediate stages shed some light on the process that was presumably a consequence of reduction in body size. In the tree including Recent taxa only, simplification of molar crown pattern (loss of cusps) and loss of third molar occur at once; these processes, however, occur in steps if one takes the fossils into consideration: there is first a loss of crown complexity and in a later stage there is a loss of the third molar. Callitrichines, to the exclusion of *Carlocebus carmenensis*, include the smallest platyrrhines. Although body mass is a missing entry for all the fossils, judging from the teeth, none of the fossils shown in the new intermediate nodes, has a particulary small size; body weight estimates for *Mohanamico*, taxa included within node 51, and *Lagonimico*, are all larger than callitrichine body weights (except the estimate for *C. carmenensis*), and they range between the body weights of living *Saimiri* and *Cebus*. It has been suggested, on the basis of trees built with Recent taxa only, that loss of crown complexity might be a byproduct of reduction in body size. It seems, however, that loss of crown complexity may be decoupled from reduction in body size: the former occurs before the latter.

Figures 2A and B display values of Bremer support excluding and including fossils in the data set. We see that addition of fossils substantially reduces the support for each branch.

Cebupithecia and *Nuciruptor* also provide some evidence about the evolution of some characters that seem to be intimately related to diet (Kinzey, 1992; Horovitz and Meyer, 1997; Meldrum and Kay, 1997). Pitheciins use their styliform lower incisors to harvest fruits, their sharp canines to open hard fruits, and their molars to masticate the seeds. Crenulated enamel has been argued to be advantageous in mastication (Kinzey, 1992). *Nuciruptor* displays styliform lower incisors,

but rounded lower canines; *Cebupithecia* displays long sharp canines similar in shape to those of living pitheciins, but smooth enamel, whereas pitheciins display styliform lower incisors and sharp canines, plus crenulated molar enamel. In summary, the evolution of these characters related to feeding abilities seems to have taken place in three steps: first those related to fruit harvesting appeared, then those related to fruit opening, and finally those related to the processing of the seeds contained within. As before, the Bremer support is substantially reduced in all branches with addition of the fossil taxa (fig. 2).

The position of *Carlocebus intermedius* renders those character supporting Ceboidea in figure 2A ambiguous while only one unambiguous character supports Ceboidea + *C. intermedius* (node 57) and another supports Ceboidea (node 56). The characters supporting Ceboidea in figure 2A are the position of the entoconid on M_1 on the talonid corner (as opposed to being separated from the talonid corner by a sulcus; ch. 54); M_3 being subequal in length to P_4 (from a primitive condition of a longer M_3; ch. 58); loss of a lingual heel on I^1(ch. 60); and relative lengths of M^3 and P^4 changing from subequal to M^3 being shorter than P^4 (ch. 78). When one adds the fossils to the data set (fig. 2B), the origin of the clade Ceboidea + *C. intermedius* is marked by the presence of a vertex in the area where the lingual cingulum terminates mesially (ch. 38); and Ceboidea turns out to be supported by an enlarged P_2 (ch. 42). Given the large number of missing entries for *Carlocebus intermedius*, it does not add much information to our understanding of character distribution in the basal nodes of its clade. In addition, its unstable position in morphology-based trees suggests caution in considering its position in the simultaneous analysis tree as reliable.

Branch Support Versus Taxonomic Completeness

From the examples described in the previous section, it is apparent that clades strongly supported by many synapomorphies become weakly supported when fossil taxa are added. It is frequently the case that biologists are interested in the degree of character support of different branches on a tree. A strong branch support gives some kind of confidence that a group is actually an historically natural group and that the phylogeny is fairly robust to falsification. In this study, however, there are cases in which a strong character support for a clade is apparently an artifact of extinctions; characters that appear clustered in specific nodes when Recent taxa only are included in the analysis are actually scattered among several nodes when the tree includes fossils, and each node receives just a small fraction of that seemingly strong and concentrated support.

Several factors may be responsible for the decrease of Bremer support with addition of fossils; for example: (1) characters are spread out along several branches; (2) fossils introduce some additional homoplasy into the tree (as addition of taxa, either Recent or fossil, usually do); and (3) fossils have many missing entries and therefore have a higher potential to accommodate many different locations on the tree, all equally parsimonious. A single most parsimonious tree was obtained in this case, but when one explores longer trees for the Bremer support calculation, trees start to proliferate. When the strict consensus is computed, clades collapse with a few additional steps.

Novacek (1991) discussed the weakening of branch support in relation to the addition of homoplasy when including new taxa in a data set. When a taxon X is added to a hypothetical data set and it turns out to be the sister group of clade AB, it splits the support that clade AB had in two nodes, in addition to adding homoplasy. Both factors combined have the effect of reducing the Bremer support for clade AB.

The weakening effect, however, is a possibility even if the added taxa display no homoplasy at all and are coded for the entire set of characters. A data set was designed (appendix 3) which yielded the tree shown in figure 6A. A new taxon was added to the data set; it did not increase the amount of homoplasy and the topology obtained was the same for the preexisting taxa, but the Bremer support was weakened for its sister group (fig. 6B).

In conclusion, stability of some branches

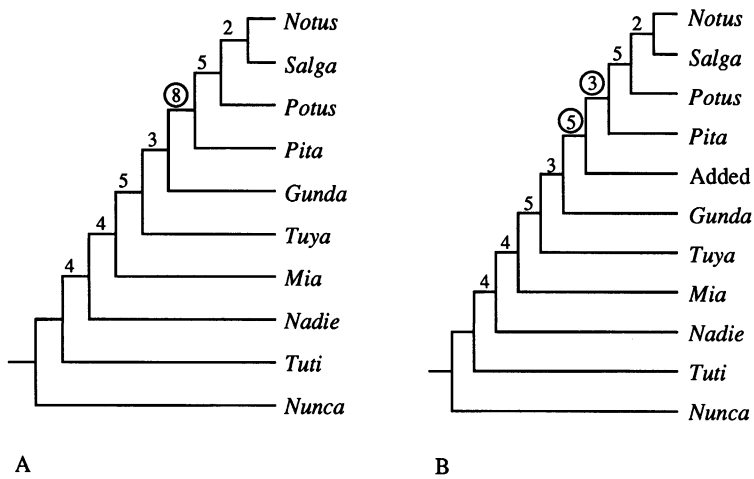

Fig. 6. Trees obtained with hypothetical data set shown in appendix 3, comparing Bremer support values (numbers above branches), **(A)** with a 10 taxa data set and **(B)** adding taxon "Added 1" to data set A. Both trees have the same amount of homoplasy, in other words taxon "Added 1" does not add any steps to the previous tree (both trees of CI = 0.81 and RI = 0.91).

on a cladogram may not be related to reliability but with extinction events or poor taxonomic sampling. Weakly supported groups are in some cases the byproduct of intensive taxonomic sampling (Recent and/or extinct) and, accordingly, they present excellent opportunities to investigate character evolution. Addition of new taxa, either living or extinct, gives a more accurate account of the diversity of a group, and provides new information about character optimizations and tree topology. Conversely, well supported groups may in some cases be an artifact of limited taxonomic sampling.

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APPENDIX 1

Character List

NOTE: See Horovitz and MacPhee (1999) for discussion on characters 1 through 79 and 86. Characters that are multistate and nonadditive are noted; all others are additive.

(1) Offspring per birth, number (Wislocki, 1939; Hill, 1926): 0 = one, 1 = two.

(2) Lumbar vertebrae, number (Erikson, 1963): 0 = more than five, 1 = five or fewer.

(3) External thumb (Pocock, 1925): 0 = absent or reduced, 1 = present.

(4) External tail: 0 = absent (not projecting), 1 = present.

(5) Tail, ventral glabrous surface (Pocock, 1925): 0 = absent, 1 = present.

(6) Claws on all manual and pedal digits except hallux (Buffon, 1767): 0 = absent, 1 = present.

(7) Carpometacarpal joint of thumb (Napier, 1961; Fick, 1911): 0 = non-saddle, 1 = saddle.

(8) Rib cage, shape (Schultz, 1961): 0 = larger dorsoventrally, 1 = larger laterally.

(9) Ulnar participation in wrist articulations (Lewis, 1974): 0 = present, 1 = absent.

(10) Sternebral proportions (Schultz, 1930): 0 = manubrium shorter than 36% of corpus length, 1 = manubrium longer than 46% of corpus length.

(11) Orbit size (ch. 4 in MacPhee et al., 1995): 0 = smaller than 1.9, 1 = larger than 2.1.

(12) Postglenoid foramen (Horovitz, 1997): 0 = absent, 1 = reduced, 2 = large.

(13) Tentorium cerebelli, ossification (Hershkovitz, 1977; Horovitz, 1995): 0 = absent, 1 = present.

(14) Middle ear, pneumatization of anteroventral region (Horovitz, 1997): 0 = absent, 1 = present.

(15) Middle ear, paired prominences on cochlear housing (Horovitz, 1997): 0 = absent, 1= present.

(16) Pterygoid fossa, depth (Horovitz, 1997): 0 = deep, 1 = shallow.

(17) Canal connecting sigmoid sinus and subarcuate fossa (ch. 6 in MacPhee et al., 1995; Cartmill et al., 1981; Horovitz, 1995): 0 = absent, 1 = present.

(18) Vomer, exposure in orbit (Cartmill, 1978; Rosenberger, 1979b): 0 = absent, 1 = present.

(19) Ectotympanic, shape (nonadditive): 0 = tube I, 1 = ring, 2 = tube II.

(20) Temporal emissary foramen (ch. 7 in MacPhee et al., 1995): 0 = present and large, 1 = small or absent.

(21) Eyeball physically enclosed (Martin, 1992): 0 = absent, 1 = present.

(22) Cranial capacity (Horovitz, 1997): 0 = less than 15 cm^3, 1 = more than 15 cm^3.

(23) Zygomatic arch, ventral extent (Horovitz, 1997): 0 = below plane of alveolar level, 1 = above plane of border.

(24) Pterion region, contacts (Ashley-Montague, 1933): 0 = zygomatic-parietal, 1 = frontal-alisphenoid.

(25) Nasal fossa width (Horovitz, 1997): 0 = narrower than palate at level of M^1, 1 = wider.

(26) Infraorbital foramen, vertical position relative to maxillary cheekteeth in Frankfurt plane (ch. 5 in MacPhee et al., 1995): 0 = above interval between (or caudal to) M^1 and P^4, 1 = above interval between P^4 and P^3, 2 = above (or rostral to) anteriormost premolar.

(27) Zygomaticofacial foramen, size relative to maxillary M^1 breadth (ch. 1 in MacPhee et al., 1995): 0 = small, 1 = large.

(28) Deciduous I_2, shape (nonadditive) (Horovitz, 1997): 0 = bladelike, lingual heel absent, 1 = bladelike, lingual heel present, 2 = styliform, lingual heel absent.

(29) Relative height of I_1-I_2 (Rosenberger, 1979b): 0 = I_1 absent, 1 = I_1 lower than I_2, 2 = I_1-I_2 subequal.

(30) Alignment of I_1-I_2 (Hershkovitz, 1970, 1977; Rosenberger, 1979b): 0 = transversely arcuate, 1 = staggered.

(31) Permanent I_1-I_2, shape (Rosenberger, 1979b): 0 = spatulate, 1 = styliform.

(32) Mesostyles and distostyles of I_1-I_2 (Hershkovitz, 1977): 0 = absent, 1 = present.

(33) Diastema between C_1 and I_2 (Rosenberger, 1979b): 0 = absent, 1 = present.

(34) Root of C_1, shape (ch. 11 in MacPhee et al., 1995): 0 = rounded/suboval, 1 = highly compressed.

(35) Lingual cingulum on C_1, completeness: 0 = complete, 1 = incomplete or absent.

(36) Lingual crest on C_1, sharpness (Kay, 1990): 0 = rounded, 1 = sharp.

(37) Lingual cingulum on C_1, mesial elevation of (Horovitz, 1997): 0 = not elevated, 1 = elevated.

(38) Lingual cingulum on C_1, forming spike on mesial edge of tooth (Horovitz, 1997): 0 = absent, 1 = present.

(39) Buccolingual breadth of alveolus of C_1, compared to P_4 (Horovitz, 1997): 0 = C_1 larger than P_4, 1 = C_1 smaller than P_4.

(40) Deciduous P_2, angle subtended by distal portion of mesiodistal axis and postprotocristid (Horovitz, 1997): 0 = smaller than 45, 1 = larger than 45.

(41) Deciduous P_2, cross-sectional shape (Horovitz, 1997): 0 = rounded, 1 = mesiodistally elongated.

(42) Size of P_2, relative to P_3 and P_4 (Horovitz, 1997): 0 = P_2 smallest in premolar series, 1 = P_2 not the smallest.

(43) Deciduous P_3, metaconid (Kay and Meldrum, 1997): 0 = absent, 1 = present.

(44) Protoconid of P_3, size relative to P_4 protoconid (Horovitz, 1997): 0 = P_3 and P_4 protoconids subequal, 1 = P_3 protoconid largest.

(45) Talonid of P_3 (Horovitz, 1997): 0 = larger than P_2 talonid, 1 = subequal to P_2 talonid.

(46) Metaconid height of P_3, relative to protoconid height (Rosenberger, 1979b): 0 = metaconid absent, 1 = metaconid lower than protoconid, 2 = metaconid and protoconid subequal, 3 = metaconid taller than protoconid.

(47) Metaconid of P_4, height relative to protoconid height (Rosenberger, 1979b): 0 = metaconid lower than protoconid, 1 = metaconid and protoconid subequal, 2 = metaconid taller than protoconid.

(48) Hypoconid of P_4 (Kay and Williams, 1994): 0 = absent, 1 = present.

(49) Entoconid of P_4 (Kay and Williams, 1994): 0 = absent, 1 = present.

(50) Number of premolars: 0 = two, 1 = three.

(51) M_1 projection of distobuccal quadrant (DB complex) (ch. 14 in MacPhee et al., 1995): 0 = not projecting, 1 = projecting (crown sidewall hidden in occlusal view).

(52) M_1 intersection of oblique cristid and protolophid (ch. 15 in MacPhee et al., 1995): 0 = intersects protolophid buccally, directly distal to apex of protoconid, 1 = intersects protolophid more lingually, distolingual to apex of protoconid.

(53) M_1 buccal bulging of protoconid (Horovitz, 1997): 0 = absent, 1 = present.

(54) M_1 entoconid position (Rosenberger, 1977): 0 = on talonid corner, 1 = distally separated from talonid corner by sulcus.

(55) M_1/M_2 buccal cingulum (Kinzey, 1973): 0 = absent, 1 = present.

(56) M_2 trigonid/talonid relative height (Kay, 1990): 0 = trigonid taller than talonid, 1 = subequal.

(57) M_2 mesoconid (Horovitz, 1997): 0 = absent, 1 = present.

(58) M_3/P_4 relative length (Horovitz, 1997): 0 = M_3 absent, 1 = M_3 shorter, 2 = subequal, 3 = M_3 longer.

(59) Molar enamel surface (Rosenberger, 1977): 0 = smooth, 1 = crenulated.

(60) I^1 lingual heel (Rosenberger, 1979b): 0 = absent, 1 = present.

(61) I^2 orientation (Rosenberger, 1979b): 0 = vertical, 1 = proclivious.

(62) C^1 alveolus size relative to P^4 equivalent (ch. 21 in MacPhee et al., 1995): 0 = C^1 larger than P^4, 1 = C^1 smaller or equal to P^4.

(63) Deciduous P^2, trigon (Horovitz, 1997): 0 = absent, 1 = present.

(64) Deciduous P^3, hypocone (Horovitz, 1997): 0 = absent, 1 = present.

(65) P^3 preparacrista (Horovitz, 1997): 0 = absent or vestigial, 1 = present.

(66) P^4 protocone position (ch. 23 in MacPhee et al., 1995): 0 = mesial to widest point of trigon, 1 = on widest point.

(67) P^4 lingual cingulum (Kinzey, 1973): 0 = absent, 1 = present.

(68) P^4 lingual cingulum mesial projection (ch. 22 in MacPhee et al., 1995): 0 = absent, 1 = present.

(69) P^4 hypocone (Kay, 1990; MacPhee et al., 1995): 0 = absent, 1 = present.

(70) P^4 and M^1, relative buccolingual breadth

(MacPhee et al., 1995): 0 = P^4 narrower than M^1, 1 = P^4 subequal to or wider than M^1.

(71) M^1 mesostyle/mesoloph (nonadditive) (Kinzey, 1973): 0 = absent, 1 = mesostyle present, 2 = mesoloph present.

(72) M^1 hypocone/prehypocrista presence (Rosenberger, 1979b; ch. 30 in MacPhee et al., 1995): 0 = hypocone and prehypocrista present, 1 = hypocone present and prehypocrista absent, 2 = hypocone and prehypocrista absent.

(73) M^1 postmetacrista slope (ch. 26 in MacPhee et al., 1995): 0 = distobuccal slope, 1 = distal or distolingual slope.

(74) M^1 mesiodistal alignment of protocone and hypocone (ch. 27 in MacPhee et al., 1995): 0 = parallel, 1 = hypocone lingual.

(75) M^1 pericone/lingual cingulum (ch. 29 in MacPhee et al., 1995): 0 = absent, 1 = lingual cingulum only, 2 = distinct pericone on lingual cingulum.

(76) M^2 hypocone (Rosenberger 1979b; ch. 32 in MacPhee et al., 1995): 0 = absent, 1 = present.

(77) M^2 cristae on distal margin of trigon (nonadditive) (ch. 31 in MacPhee et al., 1995): 0 = cristae form distinct, continuous wall between protocone and metacone, 1 = cristae interrupted by small fossa or do not form distinct wall, 2 = cristae absent or differently organized.

(78) M^3/P^4 relative mesiodistal length (Rosenberger 1979b; Horovitz, 1997): 0 = M^3 absent, 1 = M^3 shorter than P^4, 2 = M^3 and P^4 subequal, 3 = M^3 longer than P^4.

(79) Maxillary molar parastyles (Horovitz, 1997): 0 = absent, 1 = present.

(80) Buccolingual width of maxillary M^3 compared to M^1 (Horovitz, 1997): 0 = M^3 at least 0.67 of M^1, 1 = M^3 almost 0.5 of M^1.

A ratio of buccolingual width of M^1 over M^3 was computed and a gap in distribution was found between the ratios for *Callimico* and *Lagonimico* and all the other taxa for which these measurements could be made. *Callimico* and *Lagonimico* had character state 1. This character was scored on taxa for which both teeth were available for the same individual.

(81) Buccolingual width of M_1 talonid plus buccal cingulum compared to talonid alone (Horovitz, 1997): 0 = cingulum narrow, 1 = cingulum wide.

This character was only scored for taxa that displayed a buccal cingulum. Measurements were made just distal to the protolophid. A ratio of talonid plus buccal cingulum width over talonid width alone was computed for every taxon. Those that had a ratio smaller than 1.5 were scored as 0, and those with a ratio larger than 1.6 were scored as 1.

(82) Mandibular molar M_1 buccolingual talonid width relative to the trigonid (Rosenberger, 1979b): 0 = trigonid is 0.8–1 times talonid, 1 = trigonid is 0.6–0.7 times talonid.

Measurements were made from the protoconid to the metaconid for the trigonid, and from the hypoconid to the entoconid for the talonid. *Alouatta*, *Stirtonia tatacoensis*, and *Tremacebus* were the only taxa with state 1.

(83) Presence of vertical prominence on C_1 (Horovitz, 1997): 0 = absence, 1 = presence.

The enamel on buccal side of the canines extends far lower than on the lingual side, on the surface of a vertical prominence on the canine. Taxa that have this character are *Soriacebus*, *Callithrix*, *Cebuella*, and *Cebus*.

(84) Relationship of zygomatic arch with inferior orbital fissure (Setoguchi and Rosenberger, 1987): 0 = independent, 1 = zygomatic arch front limit of inferior orbital fissure.

In most taxa, the inferior orbital fissure has no relationship to the zygomatic arch. However in *Tarsius* and *Aotus*, the orbit is so enlarged that it reaches the zygomatic arch ventrally; this structure is dorsoventrally compressed and it constitutes part of the front limit of the inferior orbital fissure. This region is partially preserved in *Aotus dindensis* and the zygomatic arch is dorsoventrally compressed as in living *Aotus* species and *Tarsius*, in such a way that it seems to have been the front limit of the inferior orbital fissure (Setoguchi and Rosenberger, 1987).

(85) Prominence on P_2 crown buccal wall (Horovitz, 1997): 0 = absent, 1 = present.

A few taxa display a large vertically elongated bulging on the buccal wall of P_2, in such a way that the enamel on the buccal wall of the tooth extends lower than on the lingual wall, typical in *Soriacebus*. *Carlocebus carmenensis* and *C. intermedius* do not share this condition; they do display a bulging surface but in the shape of a belt along the bottom of the crown, which does not extend lower than the lingual wall of the tooth.

(86) Ventral flexion of the skull (airorhynchy) (Horovitz and MacPhee, 1999): 0 = absent, 1 = present.

APPENDIX 2

Matrix of Morphological Characters

	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Tarsius	0	0	1	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	2	0	0	0
2	Leontopithecus	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0
3	Saguinus	1	0	1	1	0	1	0	0	0	0	0	2	1	0	1	1	1	0	1	1	1	0
4	Callimico	0	0	1	1	0	1	0	0	0	0	0	0&1	1	0	1	0	1	0	1	1	1	0
5	Callithrix	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0
6	Cebuella	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0
7	Aotus	0	0	1	1	0	0	0	0	0	0	1	2	1	0	1	0	1	0	1	1	1	1
8	Cebus	0	0	1	1	0	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	1
9	Cacajao	0	0	1	1	0	0	0	0	0	0	0	0&1	1	0	0	1	1	0	1	1	0	1
10	Pithecia	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	1
11	Chiropotes	0	0	1	1	0	0	0	0	0	0	0	0&1	1	0	0	0&1	1	0	1	1	0	1
12	Saimiri	0	0	1	1	0	0	0	0	0	0	0	2	0&1	0	1	0	1	1	1	0	0	1
13	Alouatta	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1
14	Lagothrix	0	1	1	1	1	0	0	0	0	0	0	0&1	1	0	0	1	1	0	1	0	0	1
15	Brachyteles	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1
16	Callicebus	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	1
17	Ateles	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0&1	0	1	0	0	1
18	Homo	0	0	1	0	?	0	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	1
19	Hylobates	0	1	0	0	?	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1
20	Cercopithecoids	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
21	Aegyptopithecus zeuxis	?	?	?	1	?	?	0	?	?	?	0	2	?	0	0	0	0	?	1	?	0	1
22	Cebupithecia sarmientoi	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	1	?	1	?	?	?
23	Paralouatta varonai	?	?	?	?	?	?	?	?	?	?	1	2	?	0	1	1	?	0	1	1	0	1
24	Antillothrix bernensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	Xenothrix mcgregori	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Stirtonia victoriae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27	Stirtonia tatacoensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28	Patasola magdalenae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Lagonimico conclucatus	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	1	?	?	?
30	Mohanamico hershkovitzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	Branisella/Szalatavus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
32	Homunculus patagonicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33	Dolichocebus gaimanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	1
34	Tremacebus harringtoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
35	Soriacebus ameghinorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36	Soriacebus adrianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Carlocebus carmenensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38	Carlocebus intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	Aotus dindensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Neosaimiri/Laventiana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Nuciruptor rubricae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

APPENDIX 2. (*Continued*)

2		23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1	Tarsius	1	1	0	1	0	1	0	?	1	0	0	0	1	0	1	0	1	0	1	0	0	0
2	Leontopithecus	1	0	0	2	0	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	?	1
3	Saguinus	1	0	0	2	0	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	0	1
4	Callimico	1	0	0	2	1	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	?	0
5	Callithrix	1	0	0	2	0	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0	1
6	Cebuella	1	0	0	2	0	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0	1
7	Aotus	0	0	0	2	0	1	2	0	0	0	0	0	1	0	0&1	0&1	0	1	1	1	1	0
8	Cebus	1	0	0	2	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0
9	Cacajao	1	0	0	2	0	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
10	Pithecia	1	0	0	2	0	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0&1	1	0
11	Chiropotes	1	0	0	2	0	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0&1	1	0
12	Saimiri	1	0	0	2	0	1	2	0	0	0	0	0	1	0	0&1	1	0	0	0&1	1	1	0
13	Alouatta	1	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0
14	Lagothrix	1	0	0	1	1	1	2	0	0	0	0	0	1	0	0&1	0	0	1	0	1	1	0
15	Brachyteles	1	0	0	1	1	?	?	0	0	0	0	0	1	0	1	0	0	?	?	0	?	0
16	Callicebus	0	0	0	2	1	1	2	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0
17	Ateles	1	0	0	1	1	1	2	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0
18	Homo	1	1	?	0	0	1	2	0	0	0	0	1	0	0	?	?	1	?	?	?	?	?
19	Hylobates	1	1	0	1	0	1	2	0	0	0	0	0	1	0	1	0	0	?	?	?	1	?
20	Cercopithecoids	1	1	0	0	0	1	2	0	0	0	0	0	1	0	1	1	0	?	?	?	1	?
21	Aegyptopithecus zeuxis	1	1	?	0	0	?	2	0	0	0	0	1	1	0	1	0	0	?	?	?	?	?
22	Cebupithecia sarmientoi	?	?	?	2	0	?	?	0	?	?	1	0	1	1	0	?	0	?	?	?	?	?
23	Paralouatta varonai	?	0	1	0	1	?	?	0	0	0	0	1	1	0	1	0	1	?	?	0	?	0
24	Antillothrix bernensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
25	Xenothrix mcgregori	0	?	1	1	?	?	?	0	?	?	0	1	?	?	?	?	1	?	?	0	?	?
26	Stirtonia victoriae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27	Stirtonia tatacoensis	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	?	?	1	?	?
28	Patasola magdalenae	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	?	0	1	?	0	0
29	Lagonimico conclucatus	?	?	?	?	?	?	?	0	0	0	0	0	?	?	?	?	0	?	?	1	?	1
30	Mohanamico hershkovitzi	?	?	?	?	?	?	?	0	0	0	0	0	1	0	0	1	0	?	?	1	?	1
31	Branisella/Szalatavus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
32	Homunculus patagonicus	?	?	?	?	?	?	?	0	0	?	0	0	?	0	1	0	0	?	?	0	?	?
33	Dolichocebus gaimanensis	?	?	?	2	?	?	?	?	?	?	?	1	1	0	1	0	?	?	?	?	?	?
34	Tremacebus harringtoni	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
35	Soriacebus ameghinorum	?	?	?	?	?	?	?	1	1	?	0	0	1	0	1	0	0	?	?	1	?	1
36	Soriacebus adrianae	?	?	?	?	?	?	?	1	1	0	?	0	1	?	?	0	0	?	?	1	?	1
37	Carlocebus carmenensis	?	?	?	?	?	?	?	0	?	0	0	0	1	0	1	1	1	?	?	?	?	?
38	Carlocebus intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	0	?	?
39	Aotus dindensis	?	?	?	?	?	?	2	0	0	0	0	0	1	0	1	?	0	?	?	1	?	1
40	Neosaimiri/Laventiana	?	?	?	?	?	?	?	0	?	0	0	0	1	0	1	1	0	1	1	1	1	1
41	Nuciruptor rubricae	?	?	?	?	?	?	?	0	1	0	0	0	1	0	0	1	?	?	?	0	?	?

APPENDIX 2. (*Continued*)

	3	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
1	Tarsius	1	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	0	1	0	0	0	?
2	Leontopithecus	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	?	0	0
3	Saguinus	0	1&2	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1
4	Callimico	0	2	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	?	0	1
5	Callithrix	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
6	Cebuella	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
7	Aotus	0	2	1&2	0&1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	1
8	Cebus	0	3	2	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1
9	Cacajao	0	1	1	1	1	1	0	0	0	1	0	1	1	2	1	1	1	0	1	0	1	1
10	Pithecia	0	1	1&2	1	1	1	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	1
11	Chiropotes	0	2	1	1	1	1	0	0	0	1	0	1	1	2	1	1	1	0	1	1	1	1
12	Saimiri	0	2	1	1	1	1	0	0&1	0	0	1	0	0	1	0	0	0	0	1	1	0	1
13	Alouatta	0	1	0	1	1	1	1	1	0	1	0	0	0	3	0	1	0	0	1	0	0	0
14	Lagothrix	0	2	1	0&1	1	1	0	0	0	1	0	0	0	3	0	1	0	0	1	0	0	0
15	Brachyteles	0	1	1	0&1	1	1	1	0	0	?	0	0	0	3	0	?	0	0	?	?	0	0
16	Callicebus	0	1	1	1	1	1	0	0	0	1	0	1	0	3	0	1	0	1	1	0	0	1
17	Ateles	0	2	1	0&1	0	1	0	0	0	1	0	0	0	3	0	1	0	0	1	0	0	0
18	Homo	?	1	0	0&1	1	0	0	0	0	1	0	1	0	3	0	0&1	0	0	?	?	0	1
19	Hylobates	?	0	1	1	1	0	0	0	0	1	0	0	0	3	0	1	0	0	?	0	0	1
20	Cercopithecoids	?	0	1	1	1	0	1	0	0	1	0	0	0	3	0	1	1	0	?	1	0	1
21	Aegyptopithecus zeuxis	?	0	0	0	0	0	0	0	0	1	1	0	0	3	0	1	0	0	?	?	0	1
22	Cebupithecia sarmientoi	?	?	?	1	0	1	0	0	0	1	0	?	?	2	0	?	1	0	?	?	1	1
23	Paralouatta varonai	0	2	1	1	1	1	0	1	1	1	0	0	0	3	0	0	?	1	?	?	0	0
24	Antillothrix bernensis	?	?	?	?	?	1	0	1	?	?	?	?	?	?	?	?	?	0	?	?	?	1
25	Xenothrix mcgregori	?	?	?	?	?	1	0	0	1	1	0	1	1	0	0	?	?	1	?	?	1	1
26	Stirtonia victoriae	?	?	?	?	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	0	0	0
27	Stirtonia tatacoensis	?	1	?	0	1	1	1	1	0	1	0	0	0	?	0	?	?	?	?	?	0	0
28	Patasola magdalenae	?	1	0	0	1	1	0	1	0	0	1	0	0	1	0	0	?	?	?	?	?	?
29	Lagonimico conclucatus	0	1	0	0	0	1	0	0	0	1	1	0	0	3	0	0	?	0	?	?	0	1
30	Mohanamico hershkovitzi	0	1	1	0	1	1	0	0	0	0	0	0	0	?	0	?	?	?	?	?	?	?
31	Branisella/Szalatavus	?	?	?	?	?	1	0	0	0	?	0	0	0	?	0	?	?	?	?	?	?	?
32	Homunculus patagonicus	?	?	0&1	1	1	1	0	1	0	0	0	0	0	3	0	?	?	?	?	?	0	?
33	Dolichocebus gaimanensis	?	1	?	0	0	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?
34	Tremacebus harringtoni	?	?	?	?	?	1	0	1	0	0	0	0	?	?	0	?	?	?	?	?	?	?
35	Soriacebus ameghinorum	0	1	1	0	0	1	0	0	0	0	0	0	0	3	0	?	?	0	?	?	0	1
36	Soriacebus adrianae	0	1	1	0	0	1	0	0	0	1	0	0	0	?	0	?	?	?	?	?	0	?
37	Carlocebus carmenensis	?	?	1	0&1	0&1	1	0	1	0	0	1	0	0	?	0	0	?	?	?	?	0	1
38	Carlocebus intermedius	?	?	1	0&1	0&1	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?
39	Aotus dindensis	0	1	1	0	0	1	0	0	0	0	0	0	0	3	0	?	?	?	?	?	?	?
40	Neosaimiri/Laventiana	1	1	1	0	0&1	1	0	1	0	0&1	1	0	0	3	0	0	?	?	1	1	0	1
41	Nuciruptor rubricae	0	?	0	1	1	1	0	0	0	1	0	1	0	?	0	?	?	?	?	?	?	?

APPENDIX 2. (*Continued*)

	4	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86
1	Tarsius	1	0	0	0	0	2	0	?	1	0	0	3	1	0	1	0	0	1	0	0
2	Leontopithecus	1	0	0	0	0&1	2	1	?	1	0	0	0	1	?	0	0	0	0	0	0
3	Saguinus	1	0	0	0	0&1	2	0	?	1	0	0	0	1	?	0	0	0	0	0	0
4	Callimico	1	0	0	0	1	0	1	1	1	1	0	1	1	1	?	0	0	0	0	0
5	Callithrix	1	0	0	0	0&1	2	0	?	1	0	0	0	1	?	0	0	1	0	0	0
6	Cebuella	0&1	0	0	0	1	2	1	?	1	0	0	0	1	?	0	0	1	0	0	0
7	Aotus	1	0	0	0	0	0	1	0	0&1	1	0	1	0	0	?	0	0	1	0	0
8	Cebus	1	0	0	1	0	1	1	0	0	1	1	1	0	0	?	0	1	0	1	0
9	Cacajao	0	?	0&1	1	0	1	1	0	1	1	1	2	0	0	?	0	0	0	1	0
10	Pithecia	0	?	0&1	0	0	0	1	0	1	1	1	3	0	0	?	0	0	0	0	0
11	Chiropotes	0	?	0&1	1	0	1	1	0	1	1	1	2	0	0	?	0	0	0	0	0
12	Saimiri	1	0	0	1	0&1	1	0	0	2	1	0	1	1	0	1	0	0&1	0	0	0
13	Alouatta	0	?	0&1	0	2	1	0	0	0&1	1	1	3	0	0	?	1	0	0	0	1
14	Lagothrix	0	?	1	0	0	1	1	0	0	1	0	3	0	0	?	0	0	0	0&1	0
15	Brachyteles	0	?	0	0	2	1	1	0	0	1	?	2	?	0	?	0	0	0	0	0
16	Callicebus	1	0	1	0	0	0	1	0	1	1	1	2	0	0	?	0	0	0	0	0
17	Ateles	0	?	1	0	0	1	1	0	0	1	0	2	0	0	?	0	0	0	0	0
18	Homo	0	?	0	0	0	1	1	0	0&1	1	0	3	0	0	?	0	?	0	0	0
19	Hylobates	0	?	0	0	0	1	1	0	0&1	1	0	3	0	0	?	0	0	0	0	0
20	Cercopithecoids	0	?	0	0	0	1	1	0	0&1	1	2	3	1	0	?	0	0	0	0	0
21	Aegyptopithecus zeuxis	1	0	1	0	0&1	1	0	0	1	1	0&1	3	1	0	1	0	?	0	0	0
22	Cebupithecia sarmientoi	1	0	?	0	0	0	1	0	1	1	?	1	1	?	?	0	?	0	?	?
23	Paralouatta varonai	1	1	0	1	1	0	0	1	2	1	0	2	0	0	?	0	0	0	0	1
24	Antillothrix bernensis	1	1	?	1	0	1	0	1	2	1	1	?	1	?	?	?	?	?	?	?
25	Xenothrix mcgregori	1	0	0	0	0	0	1	0	0	?	?	0	0	?	?	0	?	0	?	?
26	Stirtonia victoriae	0	?	1	0	2	1	1	0	1	1	1	?	1	?	?	?	?	0	?	?
27	Stirtonia tatacoensis	0	?	1	0	2	1	1	0	1	1	1	?	1	?	?	1	0	?	0	?
28	Patasola magdalenae	?	?	?	?	0	0	0	1	2	?	?	?	1	?	1	0	?	?	?	?
29	Lagonimico conclucatus	1	0	0	0	0	2	1	?	1	0	0	1	1	1	0	0	0	?	0	?
30	Mohanamico hershkovitzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	?
31	Branisella/Szalatavus	1	0	?	0	1	1	?	?	1	?	0	?	1	?	?	0	?	?	?	?
32	Homunculus patagonicus	?	?	?	?	0	0	1	1	0&1	1	?	?	?	?	?	0	0	0	0	?
33	Dolichocebus gaimanensis	1	0	?	?	0	0	1	1	1	1	0	?	1	?	?	?	0	?	1	0
34	Tremacebus harringtoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0
35	Soriacebus ameghinorum	1	0	1	0	0	0	1	0	1	1	1	?	1	?	?	0	1	?	1	?
36	Soriacebus adrianae	?	?	?	?	0	0	?	0	1	?	?	?	?	?	?	0	1	?	1	?
37	Carlocebus carmenensis	1	0	1	0	0	0	1	0	1	1	0	?	1	?	1	0	0	?	0	?
38	Carlocebus intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
39	Aotus dindensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	?
40	Neosaimiri/Laventiana	1	0	1	0	1	1	0	0	2	1	0	?	1	?	1	0	0	?	0	?
41	Nuciruptor rubricae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

APPENDIX 3

Hypothetical Matrix for Figure 6

	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Nunca	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Notus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	Salga	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	Potus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
5	Pita	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
6	Added 1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
7	Gunda	1	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1
8	Tuya	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1
9	Mia	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
10	Nadie	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
11	Tuti	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	2	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Nunca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Notus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	Salga	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	Potus	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
5	Pita	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	1
6	Added 1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	0	0	0	1
7	Gunda	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0
8	Tuya	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0
9	Mia	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
10	Nadie	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
11	Tuti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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